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The Auditory Sensitivity of the Coyote (Canis latrans)

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THE AUDITORY SENSITIVITY
OF THE COYOTE (Canis latrans)

BY

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OF THE COYOTE (Canis latrans)

This thesis is approved as a creditable and independent investigation by a candidate for the degree, Master of Science, and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

Thesis Advisor Date

Head, Biology Dept. Date

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TABLE OF CONTENTS

Table of Contents, con't

LIST OF FIGURES

LIST OF TABLES

CHAPTER I

INTRODUCTION

Problem Statement

The coyote (Canis latrans) is probably the most controversial predator species in the United States. On one side of the controversy are the agricultural interests, the foremost of which is the sheep industry. Coyotes prey on cattle, goats, turkeys and other domestic stock, but the major losses involve coyotes killing sheep (Balser, 1974). On the other side of the controversy are the preservationists, who are concerned about wildlife and the environmental effects of widespread predator control programs.

Early in the 1970's the public became increasingly alarmed at the cost of Federal predator control and at the large amounts of poisons distributed for predator control. Growing public pressure, along with the 1971 Predator Control report submitted by a Presidential Advisory Committee, chaired by Stanley A. Cain (Cain et al., 1972), led to an executive order by former President Nixon in February of 1972 which prohibited chemical control of predators by federal agencies. More importantly it prohibited the use of chemical poisons on federal land. Poisoning was one of the most commonly used methods for controlling predators on the large areas of federal land that are leased for grazing. The Environmental Protection Agency also banned all interstate shipments of chemicals used for predator control and cancelled the registration of all toxicants used for that purpose.

Following these actions there was increased interest in coyote research. The livestock industry called for alternative methods of controlling coyote predation. Studies were initiated to investigate the biology, ecology, and behavior of the coyote. Damage assessments were begun to determine the true impact of coyote predation on livestock and researchers also began investigating nonlethal methods of reducing coyote predation.

South Dakota State University (SDSU) was assigned by the Agricultural Research Service, U.S. Department of Agriculture to research and develop audio repellents to deter coyote predation. Researchers were to determine audio signals having the greatest effect on coyotes and design a signal generator that would be practical in the field. Researchers from the departments of electrical engineering, psychology, and wildlife biology participated in the multidisciplinary project.

While pursuing the primary question of which pure tone frequencies or which complex acoustic signals might serve as effective deterrents, several questions arose. What range of frequencies is audible to the coyote? And how sensitive is the coyote to various frequencies?

Objective

The objective of this study, then was to determine the auditory sensitivity of the coyote so that optimal repellant frequencies might be selected for further study. The procedures, apparatus, and methodology that were developed for measuring the audiogram using two different approaches are discussed in the following text. The first approach was to use changes in respiratory patterns as an indicator of the coyote's auditory sensitivity. The second was to determine the audiogram using operant behavioral techniques.

Hypotheses

This study was based on the following hypotheses:

1. The coyote's maximum auditory sensitivity range would approximate that of the dog.
2. The maximum auditory sensitivity of both the coyote and the dog was in the range of 650 Hz to 40,000 Hz.
3. Changes in respiration patterns could be utilized to indicate auditory sensitivity in the dog.
4. Changes in respiration patterns could be utilized to indicate auditory sensitivity in the coyote.
5. The dog's audiogram could be determined using operant behavioral conditioning.
6. The coyote's audiogram could be determined using operant behavioral conditioning.

CHAPTER II

LITERATURE REVIEW

Due to the pioneering nature of this study, an exhaustive search of the literature was conducted to review a wide spectrum of related topics. A computerized bibliograhic reference retrieval service was utilized in addition to the usual literature review procedures. Some studies on auditory sensitivity in domestic dogs were listed in the Bibliography on Hearing (Andreyev, 1928; Anrep, 1920; Dworkin, 1934); Culler & Mettler, 1934; Griden, 1935; Lipman & Grassi, 1942). These were compiled by the psychoacustic laboratory at Harvard University. Horn and Lehner (1974) did investigate the scotopic sensitivity of the coyote, using behavioral techniques; however, no studies specifically investigating the auditory sensitivity of the coyote were found. The literature did reveal that there were two general approaches to determining an animal's sensory function. One utilized behavioral techniques and the other relied on physiological indicators.

Physiological Indicators

For many years scientists have known that under certain conditions body parameters change when external stimuli are presented to an organism. The main advantage of these physiological indicators is that they do not require long periods of training or conditioning.

One of these physiological indicators is evoked cochlear potentials. This procedure required surgery to expose the inner ear and the cochlear potentials were detected utilizing either a platinum foil or a silver bead electrode on the round window membrane along with an indifferent electrode in nearby inactive tissue. The tone stimulus was presented to the external ear while the resulting potentials were amplified and recorded.

Wever and Vernon (1956) used electrical potentials to determining the hearing sensitivity in three species of turtle, (Clemmys insculpta) LeConte, (Chrysemys picta picta) Schneider, and (Pseudemys scripta). In addition to the potentials of the round-window membrane they also measured potentials from the dorsal part of the perilymph space close to the posterior semicircular canal and utricle and from the cranial wall of the optic capsule. However, the potentials from the round-window membrane were larger and therefore more easily detected and recorded. Potentials from the round-window membrane were also used to determine the auditory sensitivity in the cat, (Weaver, Vernon & Rahm, 1958); the marmoset (Hapale jacchus), (Wever and Vernon & Peterson, 1963); and the Gekkonid lizard (Gekko sp.), (Wever, Vernon, Peterson & Crowley, 1963) and (Wever, Peterson, Crowley & Vernon, 1964). Peterson, Pate and Wruble (1966) used cochlear potentials to compare hearing sensitivity with the structure of the outer ear in three breeds of domestic dogs. The mean auditory sensitivity function for one breed has been depicted in Figure 1.

The evoked response technique was another method for determining an organism's auditory sensitivity. The evoked response technique was based on the observation that minute changes occur in the on-going brain wave activity in humans when an auditory stimulus was introduced at the ear (McCandless & Lentz, 1968). The response was relatively small and was difficult to visualize in raw encephalographic recordings. However, small specialized computers have made it possible to record these small potentials from the intact scalp. Rose, Lambert, Morgan and Garner (1970) used EEG evoked potentials to determine the auditory acuity in the beagle. Their results, shown in Figure 2, were in agreement with Peterson et al. (1966). However, Rose and co-workers suggested conducting a study to compare evoked response thresholds with thresholds obtained using the conditioning technique. For unstated reasons they believed that the evoked response thresholds may not have reflected the best auditory sensitivity.

Respiration has also been used as an indicator of auditory sensitivity. Corbeille and Baldes (1929) used changes in respiration to test the hearing of intact and decerebate animals. They noted that prolonged stimulation caused a decrease in the respiratory rate and a decrease in the amplitude of respiration, whereas short repeated

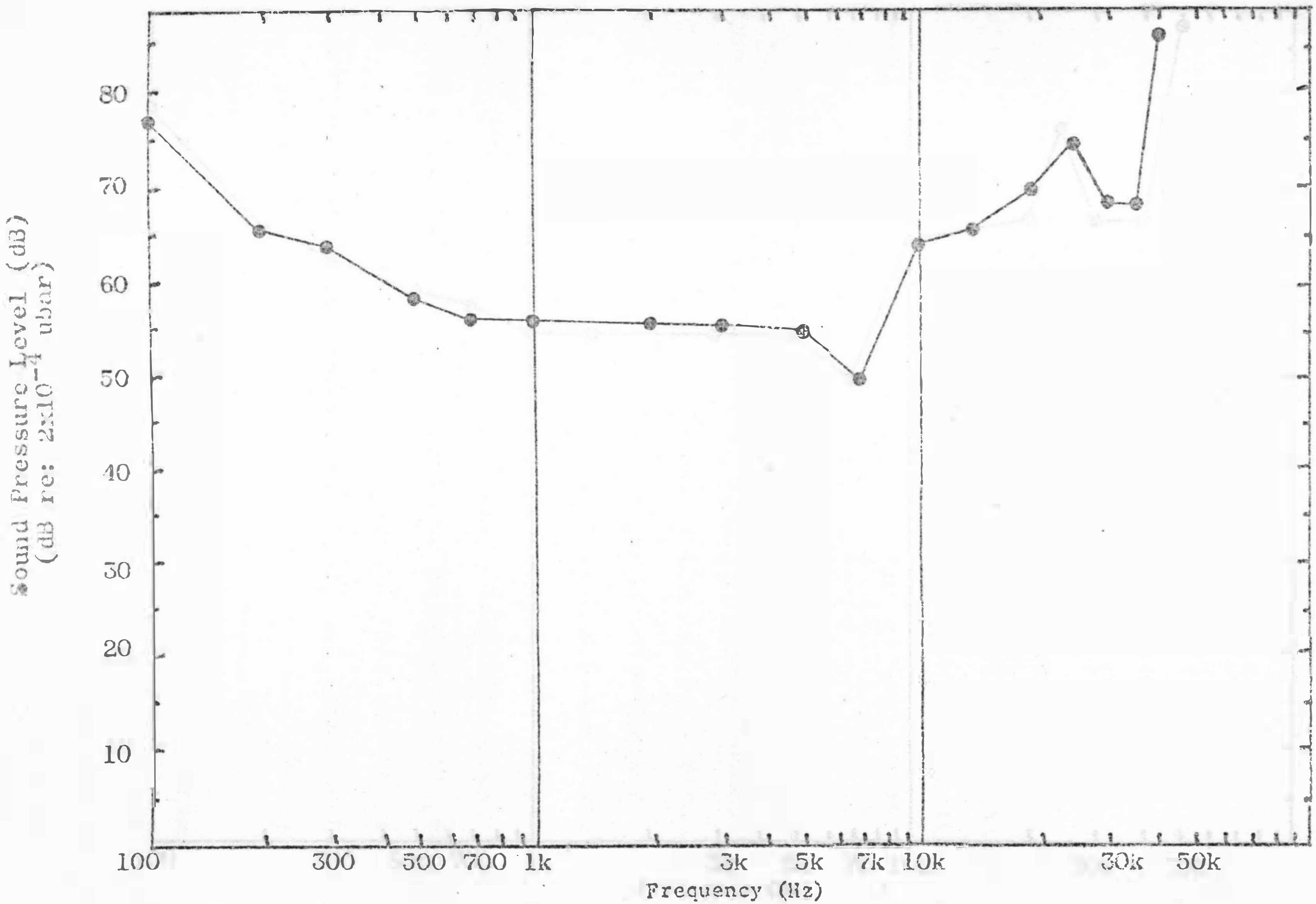


Figure 1. The mean auditory sensitivity of four beagle puppies (Peterson et al. 1966).

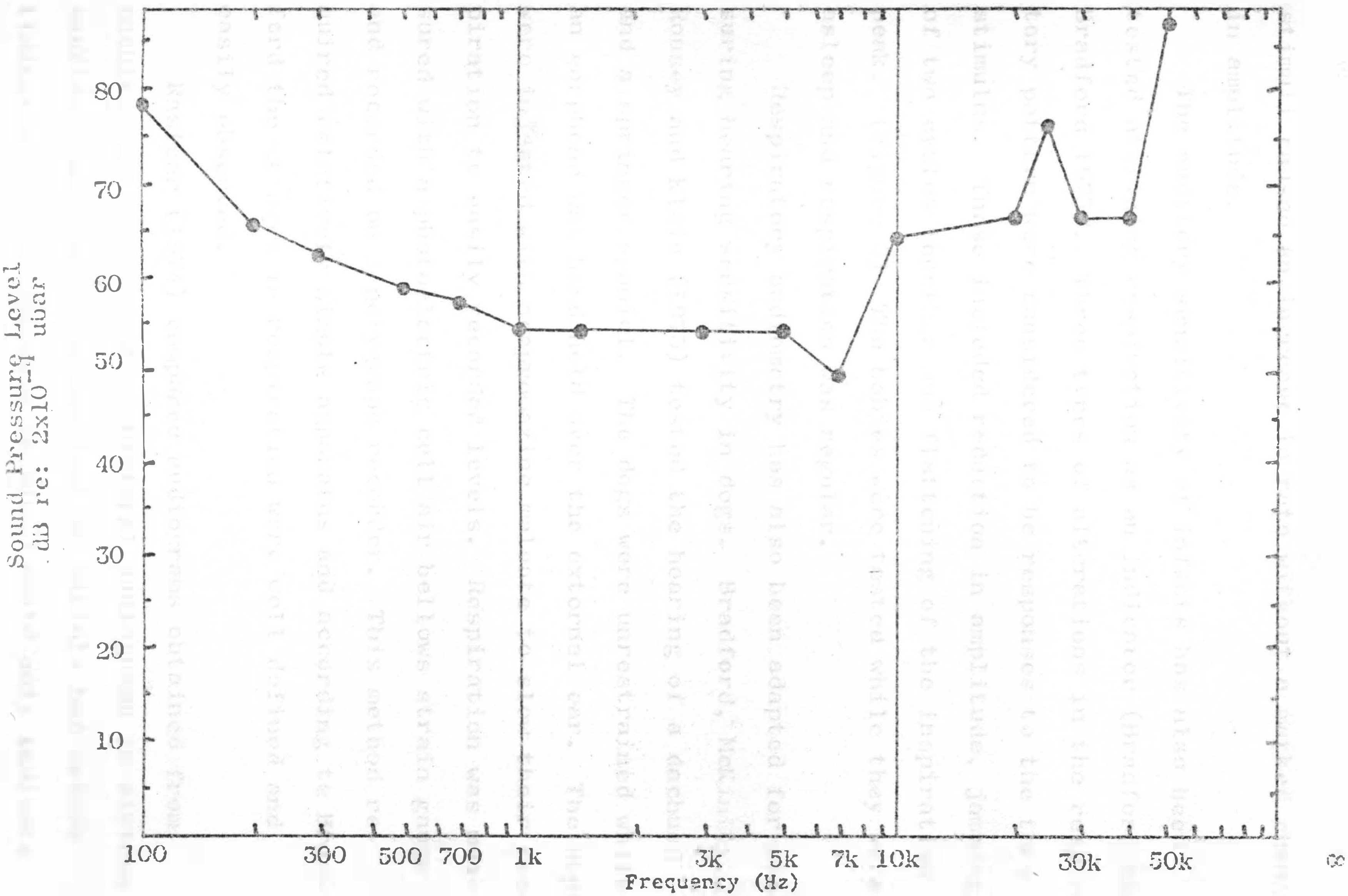


Figure 2. The mean auditory sensitivity in the beagle (Rose et al. 1970).

stimuli caused an increase in rate without a marked change in amplitude.

The auditory sensitivity of infants has also been tested utilizing respiration as an indicator (Bradford and Bradford 1975). Three types of alterations in the respiratory pattern were considered to be responses to the tone stimulus. These included reduction in amplitude, jamming of two cycles together and flattening of the inspiration peak. (Figure 3) The babies were tested while they were asleep and respiration was regular.

Respiratory audiometry has also been adapted for measuring hearing sensitivity in dogs. Bradford, McKinley, Rousey and Klein (1973) tested the hearing of a dachund and a springer spaniel. The dogs were unrestrained while an earphone was hand held over the external ear. The dogs were injected with acepromazine maleate to slow their respiration to easily recorded levels. Respiration was measured with a photoelectric cell air bellows strain gauge and recorded on a polygraph recorder. This method required relatively simple apparatus and according to Bradford the changes in respiration were well defined and easily observed.

Raslear (1974) compared audiograms obtained from cochlear potentials with behavioral audiograms in sixteen species. He found that cochlear potentials had severe limitations. The function obtained could only indicate

a. Normal respiratory pattern. One respiratory cycle (a-b); inhalation phase (1); exhalation phase (2); amplitude or depth of respiration.

b. Reduction in amplitude or depth of inspiration.

c. Jamming of two respiratory cycles together.

d. A flattening of the positive peak between the inspiration and expiration phase.

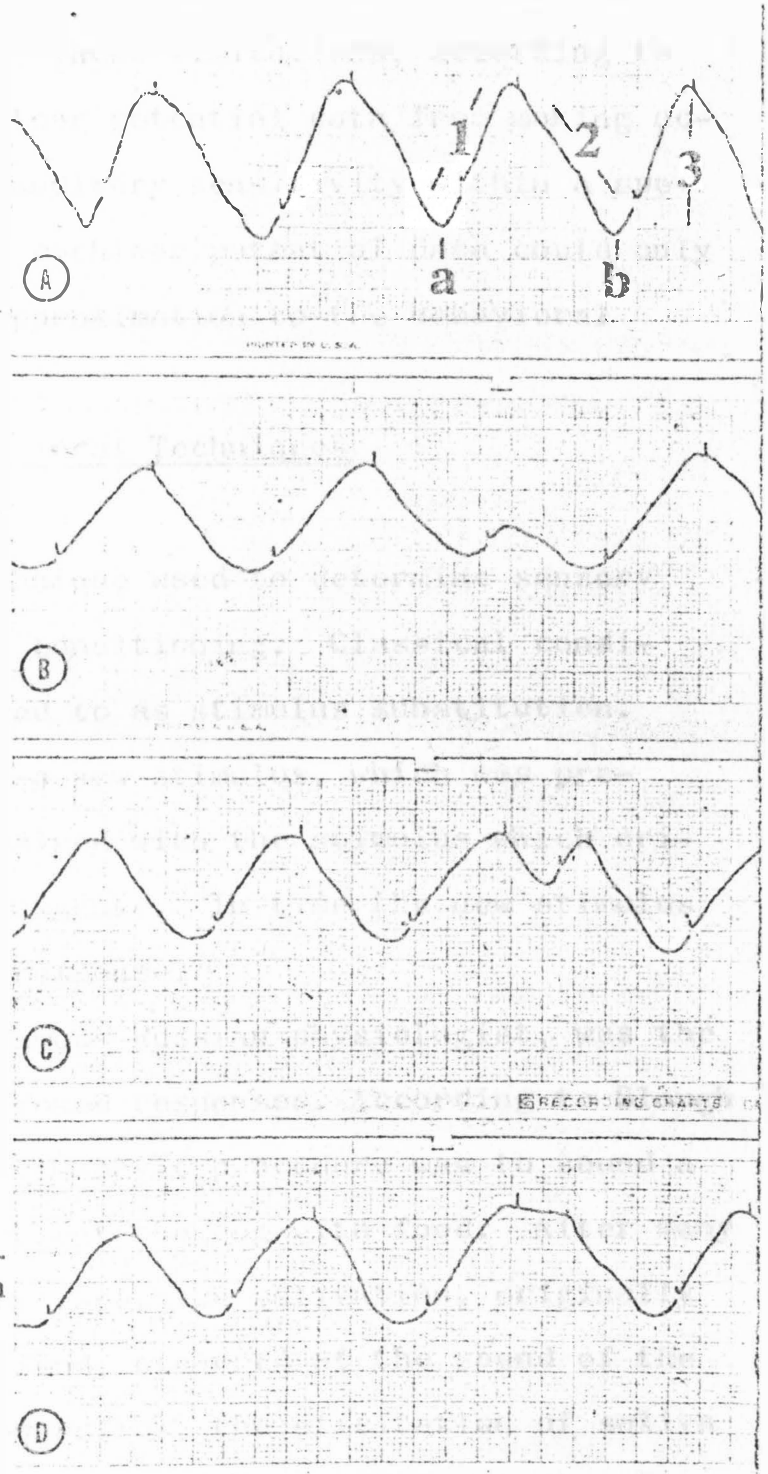


Figure 3. Changes in respiratory patterns as described by Bradford et al. (1973).

relative sensitivity and the region of maximum sensitivity could not be predicted. These limitations, according to Raslear, prevented cochlear potential data from making accurate measurements of auditory sensitivity within a species. Raslear felt that cochlear potential data could only serve as a good first approximation to the behavioral audiogram.

Behavioral Techniques

Classical conditioning:

One behavioral technique used to determine sensory functions was classical conditioning. Classical conditioning has been referred to as stimulus substitution. For a series of trials, a new stimulus, which was previously neutral, was paired with the stimulus which originally elicited the response. In time the new stimulus by itself elicited the response.

Ivan Pavlov, the famous Russian physiologist, was the first to examine conditioned responses. According to Blough and Blough (1964) Pavlov's basic procedure was to sound a tone and immediately present the dog with food. After many repetitions of this procedure, the salivation, originally a response only to the food, occurred at the sound of the tone alone. To this new reflex, the elicitation of saliva by the tone, Pavlov gave the name "conditioned reflex."

Neff and Hind (1955) used a form of classical conditioning to determine auditory thresholds of the cat. The cat was placed in a rotating cage and for a series of trials a tone was paired with a mild shock. The shock terminated when the cat ran forward in the cage. Eventually the cat became conditioned to respond to the tone and if the response occurred during the first three seconds of the tonal signal the shock was omitted. In responsive animals the threshold intensity did not vary from test to test by more than 5 dB.

Anderson, Henricson, Lundquist, Wedenberg and Wersall (1968) used classical conditioning to determine genetic hearing impairment in 55 dalmatian dogs. The dogs were conditioned by presenting clearly audible, "shock-terminated" tones until they showed signs of anxiety each time the tone was presented. The shock was then omitted and the intensity of the test tone decreased in 5 dB steps. The threshold for each frequency was taken as the lowest intensity level at which the dog responded with anxiety whether it was whining, barking, or general agitation. Conditioning was quite rapid usually after 10 to 20 repetitions.

Operant conditioning:

Another behavioral technique that has been widely used in animal psychophysics is operant conditioning. According to Blough and Blough (1964) the term operant indicates that the organism operates on its environment to generate consequences. Operant conditioning has also been referred to as instrumental conditioning because the organism's response is instrumental in gaining some reward.

B. F. Skinner, who coined the term "operant", conditioned rats to press a lever in order to receive a food pellet. Appetitive reinforcement was the term used when food or water was the reinforcing stimulus. The stimulus which initially prompted the bar-press was not known. It may have been the sight or smell of the bar, stimuli within the subject or probably a combination of these factors. If a light appeared above the bar at certain times and bar-presses were only reinforced when the light was on, the subject would eventually only press the bar when the light was on. The light had become a discriminative stimulus for the bar pressing response. Discriminative stimuli has been shown to control some aspect of the animal's behavior under certain circumstances (Blough, 1966). This control was the basis for threshold studies using operant conditioning.

Threshold studies usually require only two identifiably different responses. One of these may be interpreted as a yes response and the other as a no response. These two distinguishable response patterns may be conditioned with respect to either one or two manipulanda (Blough, 1966). Manipulanda are keys, levers or bars that the subject operates.

Heise, (195[illegible]), used a single manipulanda to determine auditory thresholds in pigeons (Columba livia). He utilized a "go, no-go" response for the simple discrimination. Tones were presented to the bird at intervals and the bird was reinforced only if it pecked the key ten times within the 15 second duration of the tone. Detection of the tone was indicated by a higher rate of pecking during the tone than in silent periods.

Schusterman, Balliet and Nixon (1972) used a similar "go, no-go" procedure to determine auditory thresholds in the California sea Lion (Zalophus californianus). The subject was reinforced with pieces of fish for emitting click vocalizations when the tone was audible and was also reinforced for remaining silent when there was no audible tone.

According to Blough (1966) reinforcement for "responding" to a positive stimulus and "not responding" to a negative stimulus may differ only superficially from procedures using two manipulanda. Blough (1959) observed that pigeons which were "not responding" to the negative stimulus were actually responding vigorously. They would perform some superstitious behavior that ended with reinforcement. One bird pecked the wall below the response key in the presence of negative stimulus, while another would wave its head in front of the key. Blough stated that more stable, uniform data may be obtained if two explicit responses were provided. This could be accomplished with a multiple discriminated response using two manipulanda.

Michelson (1959) used a multiple discriminated response with three manipulanda to study olfactory discrimination in pigeons. The bird placed its head into a cylinder through which passed a stream of air that sometimes carried an odor. It pecked the first key when an odor was presented and the second key when there was no odor. A trial terminated with reinforcement after seven correct pecks or without reinforcement after four incorrect pecks. The start of a trial was signaled by the illumination of a house light in the outer chamber and the illumination of a third key outside the odor-filled cylinder. When the pigeon pecked the third key, the airstream began to flow into the cylinder. After nine seconds, when air bearing the odorous stimulus had filled the cylinder, another peck on the third key turned off the lights outside the cylinder and turned on lights inside the cylinder. The appearance of the lights within the cylinder was the signal for the bird to put its head into the cylinder and peck the first or second key. This procuedure allowed the bird to provide itself with a controlled, stable stimulus before it was required to make the discrimination.

Smith and Smith (1972) developed a three-manipulanda technique for conditioning dogs. The three manipulanda were hinged plexiglass levers mounted on the bottom and both sides of a window which allowed access to a water dish. The dogs were first conditioned to press the bottom bar when it was illuminated to receive water reinforcement. Once pressing behavior was established on the bottom lever, the contingencies were shifted to the left and then to the right manipulanda. The final step in the training procedure was the addition of a response chaining procedure. When the bottom bar was illuminated, a response to it illuminated either the left or right manipulandum, and a response to the illuminated side lever produced reinforcement. After only 10 trials all 5 subjects met the criterion of 10 consecutive correct responses and in 50 additional maintenance trials the response chain continued to be emitted.

Another technique that has been commonly used with a multiple discriminated response has been to include some type of punishment for incorrect responses. Mohl (1968) used this technique to determine the auditory sensitivity of the common seal (Phoca vitutina vitutina). The seal controlled the onset and duration of the tone by pressing the first key. An audible tone was signaled by pressing the second key and an inaudible tone by pressing a third key. The seal was reinforced with pieces of fish for correct responses and punished for incorrect responses by a blast of air in its face.

Terhune and Ronald (1969, 1972) used almost the identical method for determining auditory thresholds in the harp seal (Pagophilus groenlandicus). Two manipulanda were used. One signaled an audible tone and one signaled that the tone was inaudible. The harp seal also received food reinforcement for correct responses and a jet of compressed air as punishment for incorrect responses.

Another form of punishment utilized is a "time out" period. Johnson (1967) used this form of punishment when determining auditory thresholds for the bottlenosed porpose (Tursiops truncatus). When the porpoise made an error the response levers were raised out of the pool for the 90 second duration of the "time out". This procedure eliminated false responses almost entirely. In fact, the subject would often not respond at all if the discrimination was a difficult one.

CHAPTER III

RESPIRATORY AUDIOGRAM

Due to the considerable length of time required to train a subject for a behaviorial audiogram, several alternative methods were considered first. The best alternative was an approach described by Bradford, et al. (1973) which utilized changes in respiratory patterns to indicate the auditory sensitivity of the dog. According to Bradford and co-workers respiratory changes were more consistent than other physiological responses and could be measured by relatively simple apparatus. Therefore, the following experiments were conducted using the basic procedure outlined by Bradford et al. (1973).

Experiment 1

Subject: The subject was a one-year old, female, black labrador dog weighing 20 kg. The animal was a friendly and energetic subject. The animal was chosen for the following reasons: 1) to test the apparatus and procedure; 2) to use an animal approximating a coyote in size; 3) to use an animal that was easy to handle, and 4) to allow for the correlation of results between the behavioral and respiratory audiograms.

Procedure: The sound was presented to the subject via a 1" ceramic transducer and a 3" diameter permanent magnet loudspeaker, both of which were mounted in an earphone. Two transducers were used to cover the frequency range more efficiently. The permanent magnet loudspeaker was used to present frequencies below 15 kHz and the ceramic transducer was used for frequencies 15 kHz and above. The signal to the transducers was produced by a Hewlett-Packard Model 233 A signal generator.

The audio switch was a critical component because it was required to consistently pass all signals as well as be noiseless (it could not produce "pops" or cracking noise) during the "on" and "off" switching operation. A reed relay was used to switch the audio signal onto the speaker lines or short the speaker lines to stop the signal. A diode, resistor, capacitor arrangement was used to eliminate any extraneous clicking or popping noises when the switch was activated. The circuit actually ramped the voltage from approximately zero volts to a final value of approximately one to two volts depending on the sound level desired. The time to reach full voltage was approximately 0.1 seconds after turn on. (Dracy, Sander, Burke & Hanson, 1975).

The sound pressure level (SPL) was measured by a Model 2107 Bruel and Kjaer (B&K) sound level analyzer via a B&K Type 4133 microphone mounted in the ear piece. The sound level analyzer was used alone for frequencies below 20 kHz. A Krohn-Hite Model 3202 filter was connected as an external band-pass filter to extend the analysis of sound levels to the range of frequencies from 20 kHz to 40 kHz. This apparatus monitored the signal via the calibrated microphone and utilized a bandpass filter to isolate and measure the sound level of only the frequency desired and chosen by the internal or external filter. A Hewlett-Packard Model 5212 frequency counter was used to measure and display the frequency of the tone stimulus.

Following Bradford's procedure (Bradford, 1975) 0.5 mg / kg acepromazine maleate was administered to tranquilize the subject and to slow the respiratory rate to an easily recordable level. The respiratory reactions of the subject were recorded on a Brush Oscillograph. In addition to respiration heart rate was also recorded. One channel of the oscillograph recorded the ECG which was taken from the animal via three needle electrodes and amplified by a Brush Dual Channel DC amplifier.

Respiratory patterns were measured with a Baldwin Hamilton SR-4 strain gage mounted on an elastic strap which was secured around the dog's thorax. The strain gage was connected to a Brush Strain Gage Bridge, and carrier amplifier. This amplifier output was used to drive the oscillograph input and the respiration was recorded on a second channel of the oscillograph.

A third channel of the oscillograph was used to mark the onset and duration of the tone. This was accomplished by simultaneously closing a switch in the sound signal line and a switch to a fixed d-c voltage for the third channel marker.

The Tektronic's Model 5030 oscilloscope was used for additional amplification capabilities when necessary to re-produce the ECG. It was also used for monitoring all signals during the apparatus testing and during an experiment.

After respiration stabilized, each tone was presented at the start of an inhalation cycle for a duration of approximately three seconds. Frequencies of 1.25, 5, 15, 25, and 35 kHz were presented using a psychophysical procedure known as "Method of Adjustment" in which, three series of stimuli were presented for each frequency. In these series, intensities were gradually increased or decreased in 3 dB steps.

Results: The results of this first experiment were invalid for the following reasons: 1) the strain gage was not properly placed on the thoracic strap and consequently was not sensitive enough to measure sufficient amplitude for recording; 2) the subject could not be isolated and was in the same room as the control apparatus and the researchers; 3) the background sound pressure level (SPL) was 84.5 dB and caused unintentional cueing.

Experiment 2

Subject: The subject was the black labrador bitch.

Procedure: Experiment 2 followed the same procedure as experiment 1 with the following four improvements. First, the strain gage design and placement were corrected to allow more sensitive recordings of the respiratory pattern. Secondly, a more suitable location was used in which the background sound pressure level was 45 dB. Thirdly, the subject and one researcher were separated from the control apparatus and the other researchers. Fourthly, an improved switch was designed to simplify tone presentation (Dracy et al., 1975).

Each trial of the respiratory data was analyzed by three independent judges. The frequency and intensity of each trial was unknown to the judges during their analysis. The trials were designated as a "response" or "no response" using the three respiration waveform alterations described by Bradford, et al. (1973) (Figure 3) and also using an increase or decrease in respiratory rate as an indicator of auditory stimuli.

Results: The judges found that in most cases the responses were difficult to reliably categorize. The three pattern changes described by Bradford et al. (1973) were rare in the respiratory data of this experiment. A Spearman's correlation (r_s) was computed for each frequency to determine if there was a correlation between the intensity and the number of times it was judged a response. It was hypothesized that if judgments truly reflected auditory sensitivity, high intensity (above threshold) stimuli should be frequently judged as responses, and vice versa. However, the average correlation of intensity and judgments was only $r_s=0.43$. When tested statistically to determine if the value of r_s was significantly different from zero, only two of the five frequencies achieved significance at $p<.05$. Therefore, it was concluded that in this experiment respiratory patterns were not reliable indicators of auditory sensitivity. Further definition of the response criteria was needed to make reliable judgments.

Experiment 3

Subject: The subject was an adult male coyote weighing 14.5 kg. This coyote was captured as an adult and was approximately six years old.

Procedure: The same procedure was followed in experiment 3 as in experiment 2, with the following improvements: 1) 0.10 mg/kg acepromozine maleate was administered to the coyote; 2) the coyote was muzzled and restrained to prevent injury to the experimentor.

Results: A Spearman's correlation was also computed for each frequency in experiment 3. The average correlation of intensity and judgments was $r_s = .601$. However, the N was larger than in experiment 2 and again only two of the five frequencies achieved significance at $p < .05$. Therefore, the same conclusions were reached as in experiment 2.

Experiment 4

Subject: One of the major problems encountered in previous experiments was calming the coyotes sufficiently without affecting their respiration or their auditory sensitivity. A dosage of 5 mg/kg of acepromazine maleate was a satisfactory anesthetic for the domestic dog; however, 10 mg/kg was administered to two coyotes with seemingly little effect. Three coyotes were administered various dosages of sodium pentobarbital but none reached the desired level of anesthesia. Valium worked well on an adult male coyote. He weighed 14.5 kg and remained alert but quiet when administered 10 mg of valium. Two yearling coyotes each weighing approximately 11 kg remained unmanageable when administered 20 mg of valium. Consequently, only one subject was used in experiment 4, the male coyote that was used in experiment 3.

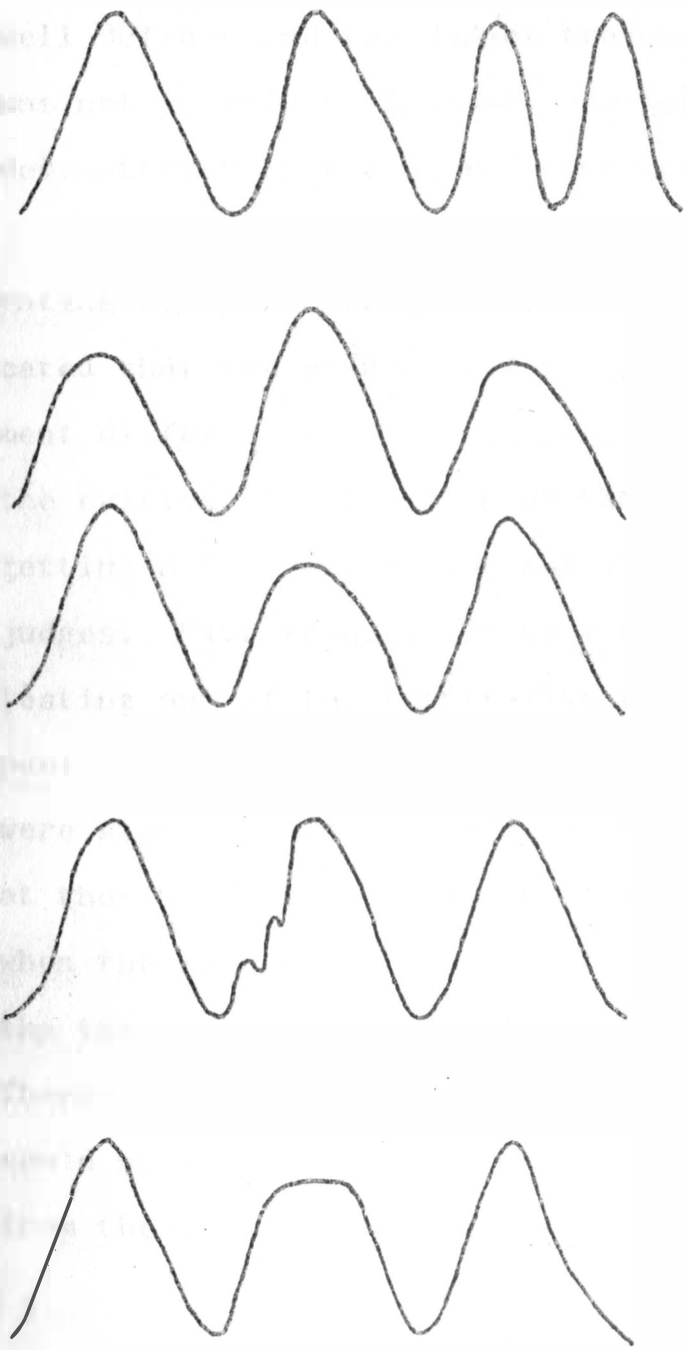
Procedure: Several more modifications were made in an effort to obtain reliable data. In order to effectively restrain the coyote during this experiment, a canvas sling was used. This aided in maintaining the proper placement of the thoracic strain gage and the earpiece.

An improved earpiece was also constructed to better conform to the coyote's ear and thus insure more consistent presentation of the tone stimulus. It was discovered that the orientation of the transducer with respect to the ear was very critical. A position shift of a few centimeters meant a difference in sound pressure level of $\pm$ 10 dB. The improved earphone and the canvas sling helped to correct this problem but did not eliminate it entirely. Also to provide more precise control of the stimulus intensities, a 3 dB-step attenuator was used.

In addition five replications of the six frequencies were tested on five different days. The six frequencies were presented in a different randomized order each day to eliminate order effects.

The major difficulty encountered in the experiments was interpreting the respiratory data. The three distinct changes described by Bradford et al. (1973) were not evident in these data. In an attempt to make the respiratory responses easier to categorize as "response" or "no response" four criteria were used. These were: 1) a change in respiratory rate; 2) a change in depth of inspiration; 3) a waver or jag in depth of inspiration; 4) or a flat inspiration peak. (Figure 4) Also "catch trials" where no tone was presented were randomly selected from the data to serve as validation trials. Then three judges examined each trial, without knowing if it were a "signal trial" or a "catch trial", and categorized each as a "response" or "no response".

Results: In order to test the null hypothesis that there was no difference between the number of "signal trials" and the number of "catch trials" that were judged as being a response, a chi square test was used. A separate statistic was computed for each of the five replications. Chi square ($df=1$, $p<.05$) values for only two of the five replications were statistically significant. However, these were in the opposite direction; "catch trials" were more often categorized as responses than "signal trials". This implies that judgments of changes in respiratory patterns were not reliable indicators of



1. Change in respiratory rate.

2. Change in amplitude.

3. Waver during inspiration.

4. Flattening of the inspiration peak.

Figure 4. Criteria for judging respiratory responses.

auditory sensitivity. Even when the rating criteria was well defined and the judges trained, the respiration data was not useable to indicate auditory sensitivity, as demonstrated by the above procedures.

A Cochran's Q test was used to compare the pattern of rating of the three judges. A significant Q value indicated that the probability of getting a "response" judgment differed among the judges. A Q value smaller than the critical level indicated that the probability of getting a "response" judgment was the same for all three judges. Five frequencies were randomly selected for testing out of the twenty-five presented during the experiment. Q (df=2) values for three of the frequencies were statistically significant at the .05 level, and two at the .001 level. This was further evidence that even when the response criteria were discussed and practiced the three judges could not reliably interpret the data. Therefore, it was tentatively concluded that no inference could be drawn about the coyote's auditory sensitivity from these respiratory data.

CHAPTER IV

BEHAVIORAL AUDIOGRAM

In a general sense the behavioral analysis of a sensory function has been referred to as animal psychophysics. The basic data of animal psychophysics are the conditioned responses of the awake, intact organism, to sensory stimulation (Stebbins, 1970). This particular animal psychophysics study dealt with the conditioned responses of canines to auditory stimuli.

Subjects

Dog 1 was the same one-year old, black labrador retriever as used in the respiratory experiments. Her temperment has been described as friendly and energetic. The research staff identified her with the "creative" title, B.D. (Black Dog).

Coyote 1 was a three-year old female, weighing 13 kg. Her temperment has been described as highstrung, aggressive, partially tamed and unpredictable. To the staff she was known as "Cody". She has been in captivity since she was a pup. She had a litter of four whelps, May 2, 1975.

Coyote 2 was also a three-year old female, weighing 16 kg. Her temperment has been described as shy, active, partially tamed and submissive. To the staff she was known as "Lil". She has been in captivity since she was a pup. She had a litter of six whelps, May 17, 1975.

The subjects were individually housed in four, 5 by 12 foot pens with small shelters attached for protection from the elements. The pens are situated adjacent to each other as shown in Figure 5. The instrumentation building was located approximately 30 feet from the pens and 20 feet from the environmental chamber. All subjects were maintained on dry dog food throughout the study.

Apparatus

Environmental Chamber:

The experiments were conducted in an environmental chamber 3 feet wide, 4 feet high and 5 feet long, constructed of ½" plywood and lined with ½" sheet rock. A smaller box nested within this chamber was the actual testing chamber. This inner chamber was constructed of ¼" masonite pegboard and 1" styrofoam and was 2 feet high, 2 feet wide and 3 feet long. The styrofoam ceiling and floor were protected from coyote damage by expanded metal. Figure 6 shows a diagram of the chamber.

This entire structure was surrounded by one layer of hay bales and was located within a screened pen. The purpose of the pen was to confine the coyotes should they escape while being placed in, or removed from the chamber. The environmental chamber provided a silent acoustic environment for frequencies above 650 Hz.

Sound pressure level in the environmental chamber, with all apparatus functioning, averaged 77 dB. However, as shown in Table 1, almost all of the ambient noise existed in the frequency range below 650 Hz. The ambient sound pres-

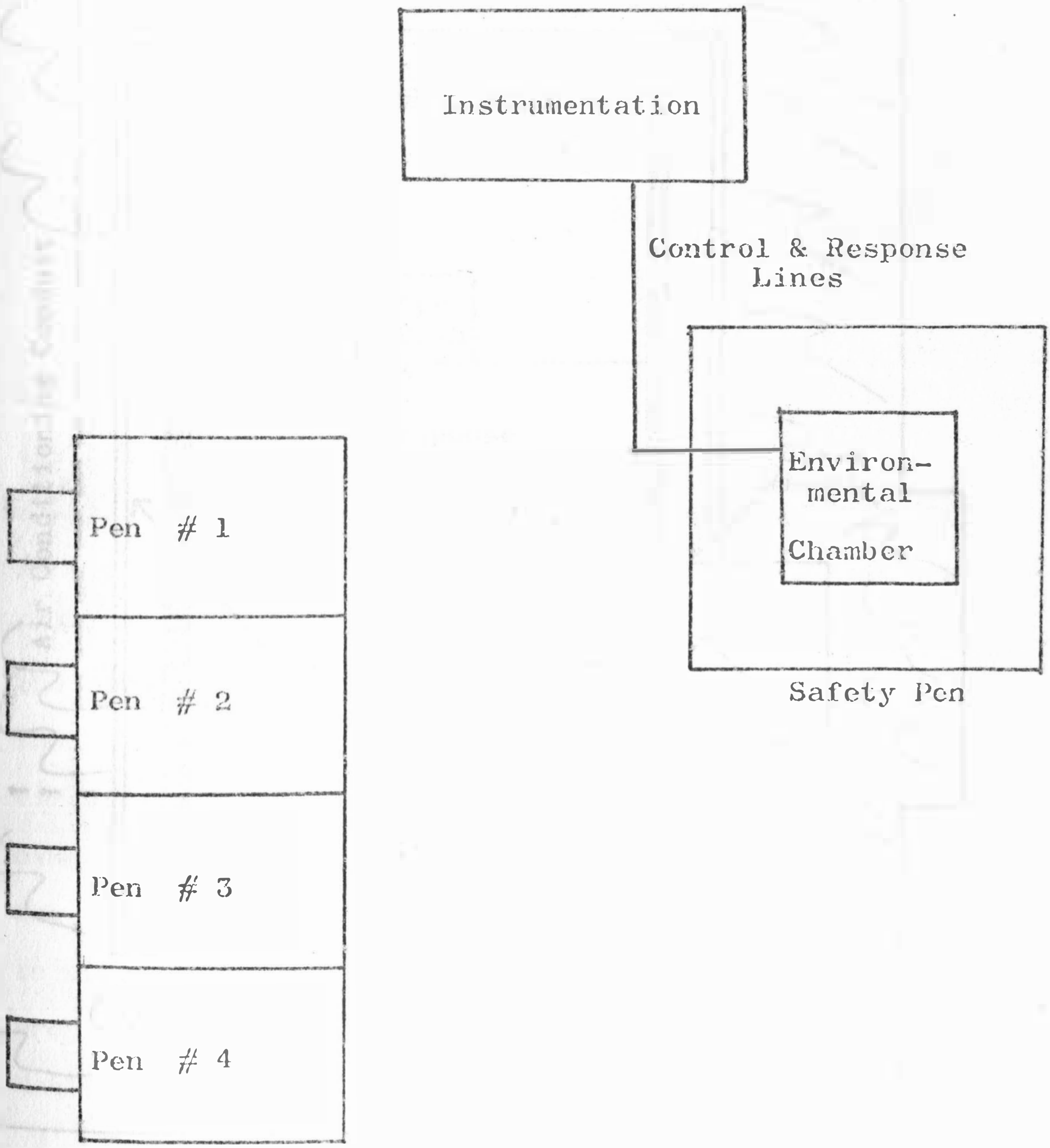


Figure 5. A schematic diagram of the Coyote Research Area.

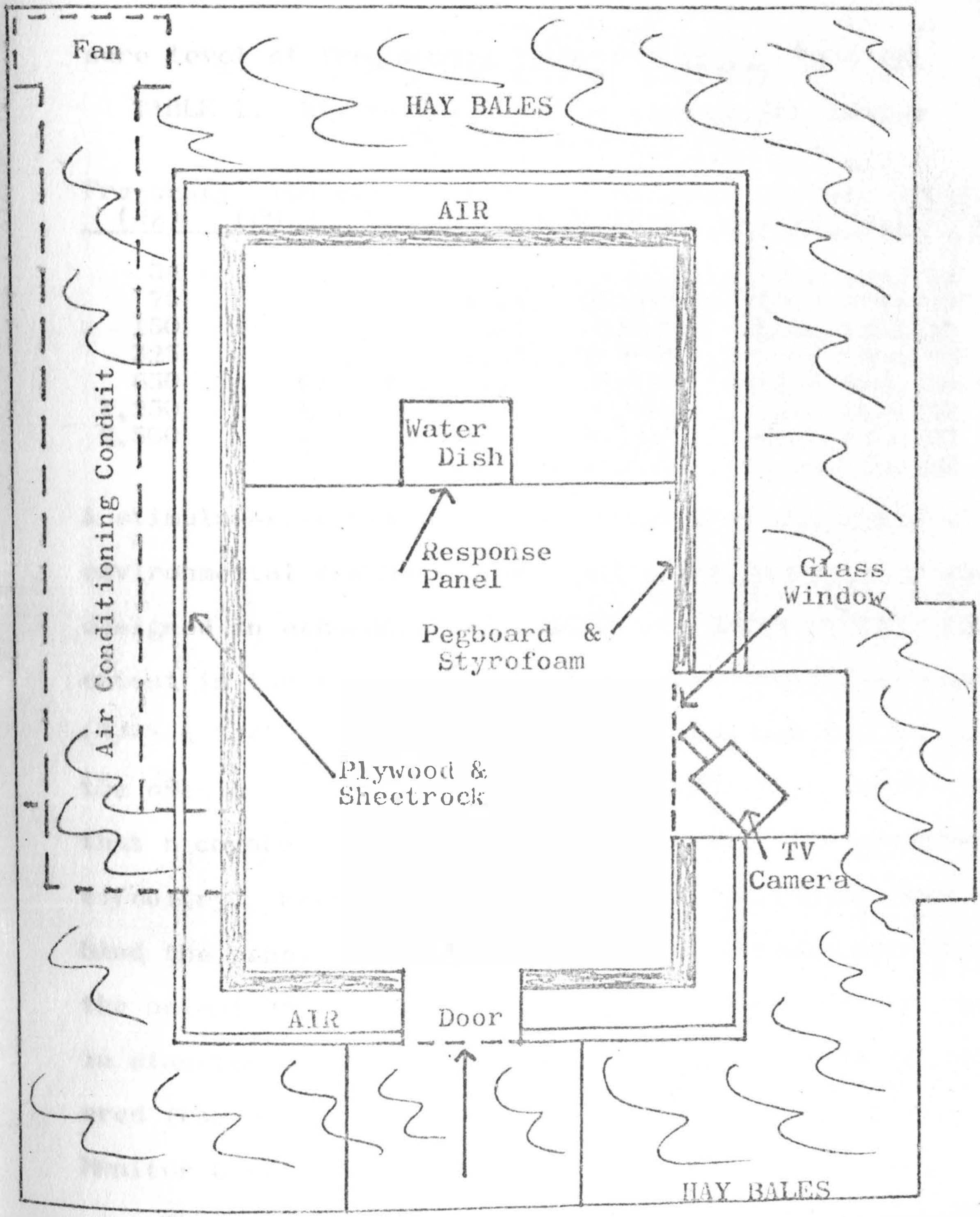


Figure 6. Schematic diagram of the environmental chamber.

sure level of frequencies below 650 Hz was 74.5 dB.

TABLE 1. Distribution of the Ambient SPL Inside the Environmental Chamber.

Frequency (Hz)	Ambient SPL (dB) (dB re: 2×10^{-4} u bar)	Frequency (Hz)	Ambient SPL (dB) (dB re: 2×10^{-4} u bar)
34	63.5	5,000	Less than 20
75	63.5	10,000	Less than 20
150	52.5	15,000	Less than 20
325	42.5	20,000	Less than 20
650	Less than 20	25,000	Less than 20
1,250	Less than 20	30,000	Less than 20
2,500	Less than 20	35,000	Less than 20
		40,000	Less than 20

A stimulus-response panel, was mounted at the front of the environmental chamber. The panel shown in Figure 7 was designed in accordance with Smith and Smith (1972). A 7" cutout in the panel was rimmed by three plexiglass bars (3/4" x 3/4" x 7") located on the bottom and two sides of the opening. These were hinged and mounted in such a way that a coyote could press the bar and activate electronic circuitry. Each bar could be separately lighted from behind the panel. By placing its muzzle through the opening the animal had access to a shallow water dish three inches in diameter. Water reinforcement was automatically delivered from a separate reservoir through a solenoid valve.

Monitor Control Unit:

The monitor control unit was designed to be multipurpose. Therefore, it was composed of many different logic modules which were interconnected in different configurations to perform the tasks desired. The logic blocks were

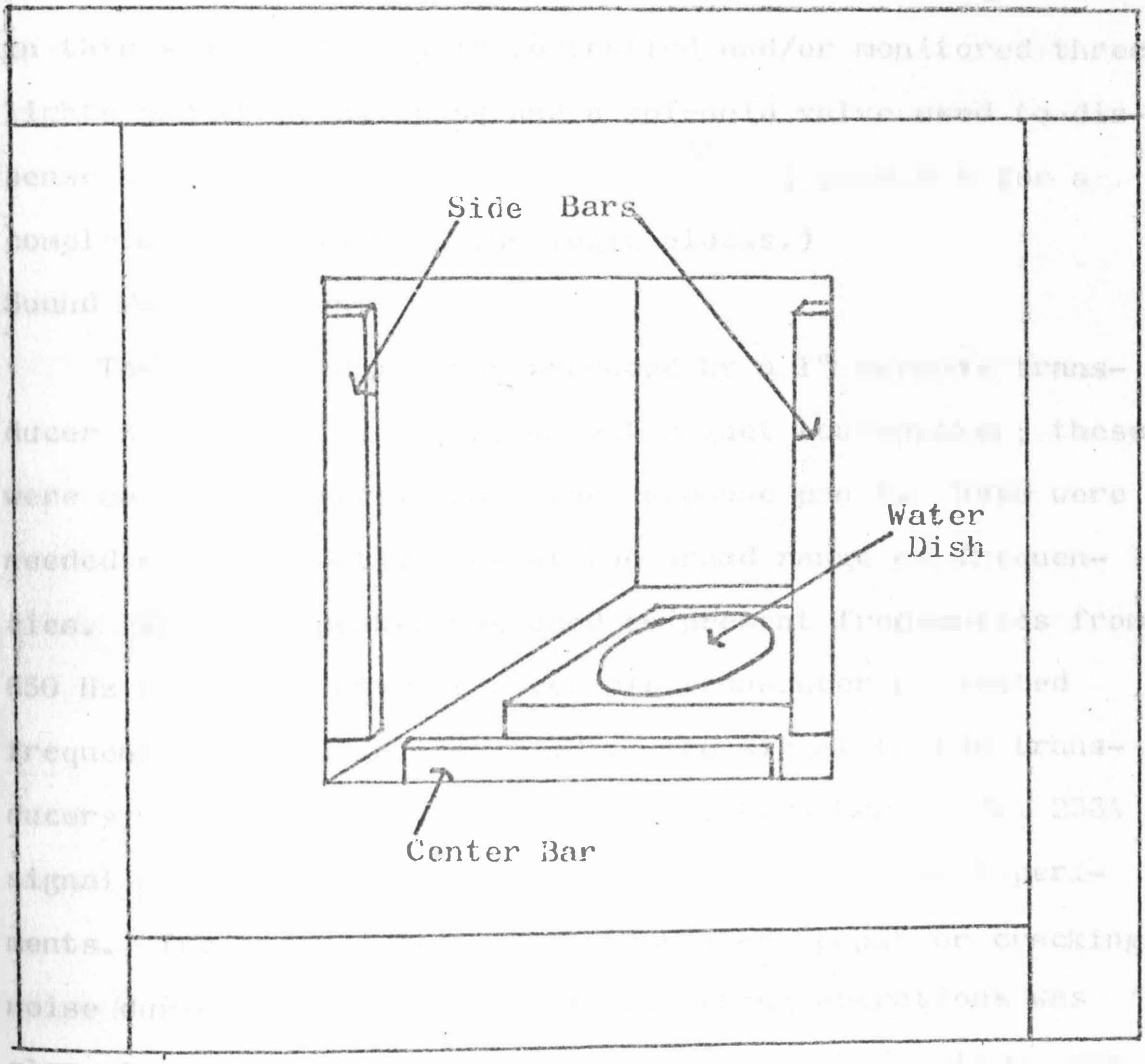


Figure 7. The stimulus response panel.

programmed for the particular training schedule required in this study. The logic controlled and/or monitored three lights and three switches and a solenoid valve used to dispense a measured amount of water. (See Appendix A for a complete description of the logic blocks.)

Sound Presentation:

The tone stimulus was produced by a 1" ceramic transducer and a 3" diameter permanent magnet loudspeaker; these were mounted directly above the response panel. Both were needed to efficiently present the broad range of frequencies. The loudspeaker was used to present frequencies from 650 Hz to 10 kHz while the ceramic transducer presented frequencies of 15 kHz to 40 kHz. The signal to the transducers was produced by the same Hewlett-Packard Model 233A signal generator that was used in the respiration experiments. The audio switch which prevented "pops" or cracking noise during the "on" and "off" switching operations was also utilized. A 0-60 dB attenuator, with 3 dB steps, was used to adjust stimulus intensity. The frequency of the tone stimulus was measured and displayed on a Hewlett-Packard Model 5212 frequency counter.

The sound pressure level was measured before each test session with a Model 2107 B&K sound level analyzer via a B&K Type 4133 microphone. The microphone was consistently placed in a fixed position in the chamber to approximate the subject's head position as he faced the response panel.

The B&K sound level analyzer was used alone to measure frequencies below 20 kHz. For the frequencies from 20 kHz to 40 kHz a Krohn-Hite Model 3202 filter was connected as an external bandpass filter. This was the same procedure that was followed in the respiratory experiments.

Television Monitor:

While in the chamber, the subjects were monitored on closed circuit television. This was accomplished with a TV camera mounted as shown in Figure 5. A video tape recorder also provided the capability of video taping training and test sessions.

Experimental Design

Blough (1966) concluded that animal psychophysics studies using behavioral indicies should include a multiple discriminated response with differential schedules. Such was the design of this experiment. For example, the animal signaled the presence of an auditory stimulus by pressing the left bar and the absence of a signal in a given trial by pressing the right bar. A further procedure required the animal to differentially respond with three presses to the left or two presses to the right. Horn and Lehner (1974) found coyotes to be capable of discriminating between visual signals by pressing on one of two foot treddles. Smith and Smith (1972) found dogs were capable of discriminating between lights by muzzle press responses. The response proposed for this experiment as recommended by other researchers seemed to be well within the behavioral repertoire of the coyote.

A second basic component of the study was the use of water reinforcement. As has been found to be true of other organisms, the coyote was able to forego food for longer time periods than water. Smith and Smith (1972) used water reinforcement with dogs. Horn and Lehner (1974) also recommended water reinforcement for coyotes, noting that longer deprevation periods were necessary for effective food reinforcement. Therefore, water was chosen as a more reliable control for training and effective maintenance of the learned response. In pilot study observation it was demonstrated that 20 ml of water per reinforcement was an effective amount for maintenance of the response.

Experimental Phases:

For the idealized situation there were three distinct phases of the experimental design. These were: Desensitization, Training, and Testing. During the Desensitization phase the animals were gradually accustomed to a daily schedule in which they had access to water only ten minutes per day. This procedure was to accustem them to working actively for water on a daily basis and to reduce their apprehension of the test chamber. Also during desensitization the subjects were gradually introduced to the experimental apparatus. These experiences were always paired with water reinforcement so that the coyote associated the chamber with the reinforcement and became accustomed to the apparatus.

The goal of the Training phase of the study was to train the completed choice behavior. The subject was first trained to perform the simple task of pressing the center bar in order to receive reinforcement. Through gradual steps the task increased in complexity until the final behavior was achieved. In each case the center bar press initiated a trial in which the animal made a choice. For awhile the discrimination choice was whether or not a side bar was lighted. After criterion performance was reached sound and light were paired together. Finally, the lights were faded out and the coyote responded to the auditory stimulus alone.

During the Testing phase the subjects were randomly presented eleven frequencies at varying intensities. The frequencies tested were: .65, 1.25, 2.5, 5, 10, 15, 20, 25, 30, 35, and 40 kHz.

This range of frequencies was chosen to sample the canine's region of maximum auditory sensitivity. It was hypothesized that the absolute frequency thresholds would extend above and below this range. These 11 frequencies were chosen as octave, ½ octave and ¼ octave steps. Emphasis was placed on the ultrasonic frequencies because they held the most promise for audio repellants. "Catch trials" where no tone was presented were also included as validation trials. The five intensities presented at each frequency were chosen to bracket the threshold values for the subject, based on pilot results. The number of trials was limited by the number of reinforcements the subject required before it became satiated.

Procedure for daily sessions:

During the testing phase of the experiment, daily procedure began with calibration of the ceramic transducer and the 3" diameter permanent magnet loudspeaker attenuator.

The input voltage was set for each frequency and the sound pressure level was measured and recorded at 0 dB attenuation. The voltages were set to produce a sound pressure level of 75 dB, $\pm$ 5 dB. This was done so the voltage setting could remain constant during testing, while the intensities to be presented could be reached utilizing the 0-60 dB attenuator. Daily calibration was necessary due to the effects of varying environmental conditions (temperature, humidity, barometric pressure, etc.) on transducer efficiency. Measurements were made with the B&K sound level analyzer as described previously in the discussion of apparatus.

Once the calibrations were made the test schedule for the day was arranged using a randomized order for presenting frequency and intensity and also using the appropriate voltage setting from that day's calibration.

Testing usually began after 5 PM. when human activity near the test site had diminished. The apparatus was allowed to warm up and was also checked to insure that it was functioning properly. The subject was leashed and led to the environmental chamber. Testing started as soon as the animal began responding and continued until the test schedule was completed or the subject was satiated. The subject was then removed from the chamber and returned to its pen. Test sessions were approximately 30 minutes.

Pilot Experiment 1

Subject:

Experiment 1 was conducted with Dog 1.

Procedure:

The first experimental session began June 15, 1975. Only one desensitization period was necessary for this animal since she willingly entered the chamber and drank readily from the reinforcement dish. During the pilot experiments two sessions were conducted each day, so training began with an evening session the same day. A trial was initiated by lighting the bottom bar. The presentation of water reinforcement depended on the animal pressing the bar within 30 seconds after illumination. Within three sessions she had learned the task to a criterion of 100% correct on 25 trials. Reinforcement was 20 ml of water. The time between trials (intertrial interval, ITI) averaged 30 seconds. During the following ten days, the training goals for the animal were: (1) To reduce her response time to the light, (2) To increase the length of testing time in the chamber, and (3) To allow only a muzzle press response. During this period of training, a session was terminated if the animal failed to respond for three consecutive trials. Mean response time was 5.78 seconds for the trials and mean session length was 12.7 trials.

The next stage of the training was initiated on the 13th training day. The dog was presented with the central light followed by a side light, then reinforcement. Initially the change increased the latency period to 42.3 seconds and reduced session length to 7 trials. The chamber was dimmed to enhance the cue value of the panel lights. On the 23rd training day, the animal had an average latency period of 10.54 seconds for twelve trials. On the 29th training day, multiple responses were required. By the 32nd training day the animal responded differentially with 6 presses to the left bar and 2 to the right with a latency period of 13.5 seconds. The time between trials was reduced to 15 seconds.

The final stage began on the 32nd day with the first introduction of sound into the chamber. An easily audible training tone of 10 kHz was paired with the left light. Her performance was poor, seemingly distracted by the sound. The session was terminated after 15 trials. This training phase was interrupted by several days of equipment malfunction, repair, and modification. After five more training days with sound and cue lights, the subject was 100% correct with a mean latency period of 13.03 seconds. On training day 38, no side lights were presented, only a center cue light and presence or absence of sound. Training frequencies of 1.25, 5, 10, and 20 kHz were randomly presented on various training days.

After ten more days of training in which the correct response rate was better than 95% and the response latency period was reduced to 5.2 seconds, the animal was judged ready for testing.

The design of the test schedule was to conduct six days of test trials with two sessions each day. The number of trials per session was limited by the number of reinforcements the subject required to become satiated. Since two speakers were used, each session was randomly selected to receive either six upper frequencies (15, 20, 25, 30, 35, 40 kHz) or five lower frequencies (.65, 1.25, 2.5, 5, or 10 kHz). Frequencies were assigned in a Latin square arrangement as were the five intensities presented at each frequency, so that order effects were controlled. The presentation of lower frequencies or upper frequencies was counter-balanced with morning or evening sessions. (See appendix B for a test schedule for one session.)

Each session contained five presentations of each frequency. Each of these presentations was a different intensity, randomly ordered in 3 dB steps. The intensities chosen were based on pilot study information so as to bracket the presumed threshold value observed and/or reported by Rose et al. (1970) for dogs.

In addition, sufficient no-sound trials were randomly added to the sequences to provide "catch trials" or validity trials. The ratio of "signal trials" to "catch trials" was 3:1. The experiment was conducted with an interstimulus interval of 1.5 seconds, an intertrial interval of 15 seconds and a reinforcement schedule of 100%.

The testing phase was delayed two days and interrupted on two other days by rain which provided the animal an alternate source of water and made the reinforcement ineffective.

Results:

Table 2 depicts the mean auditory sensitivity for Dog 1. It is felt that the thresholds expressed for the frequencies .650, 1.25, 20, 30, 35, and 40 kHz closely approximate the dog's actual thresholds. However, the animal's hearing was more sensitive than the ability of the equipment to measure low power sound levels at 2.5, 5, 10, 15, 25, and 30 kHz. This was due to the configuration of the equipment.

TABLE 2

Mean Auditory Sensitivity of Dog 1

Frequency in kHz	Sound Pressure Level (SPL) in dB (re $2x10^{-4}$ bar)	Frequency in kHz	Sound Pressure Level (SPL) in dB (re $2x10^{-4}$ bar)
.65	37.5	20	27.5
1.25	32.5	25	Below 25
2.50	Below 30	30	22.5
5	Below 20	35	22.5
10	Below 20	40	32.5
15	Below 20		

Behaviorally, the work with the subject was enjoyable, but she was difficult to sustain for increased session length. The animal learned quickly, but satiated quickly to water. A paw press and muzzle press were the pronounced behavioral response repertoir.

Pilot Experiment 2

Subjects:

Coyote 1 and Coyote 2 were subjects for the experiment.

Procedure:

The coyotes desensitization phase began April 12, 1975. This phase was considerably longer for the coyotes than for the dog. For Coyote 1 this phase was 36 days, for Coyote 2 it was 80 days. The process was basically a slow acquaintance to the experimental chamber. The animal's water sites were moved closer to the chamber each day. The coyotes' extreme nervousness made this a tedious phase of the experiment.

Training began for both animals at different times. A series of similar problems was encountered with each animal. The first issue was that the coyotes failed to exhibit a muzzle press response on the center bar. Instead, they bit the bar, hit it with their paws or simply ignored the apparatus. Modifications of procedure included: making the onset of the light contingent on the animal being away from the bar; increasing the interstimulus interval; and making sure the automatic controller was reset before reinforcement if a non muzzle press occurred. Further, the panel height was raised to make a muzzle press response more likely as the animal tried to drink. Also the panel was faced with steel to render biting unpleasant. Even though several muzzle presses were observed, a paw press was the behavior that was finally allowed and reinforced. With this behavior the subjects exhibited successful conditioning in the first phase of the training. Typical performance was a 3 second latency period for a series of 25 correct trials before the animal ignored the cue lights.

The second stage of training was the introduction of side lights. This stage met with limited success. The addition of the dual response seemed beyond the behavior repertoire of the coyote. Biting, pacing, scratching and destructive aggression were observed. Several procedures were attempted to facilitate the response such as enhancing the cue value of the side lights by dimming the primary illumination in the chamber, masking off one-half of the panel opening to increase the likelihood of a response to the side lights, and addition of sound to aid discrimination. None of these were entirely successful, although Coyote 1 achieved a differential response which was correct approximately 60% of the time.

Results:

After the animals failed to learn the desired behavior, the experiment was terminated 214 days after it began. The proceedings were analyzed and the following were concluded: (1) that the light indicating reinforcement was too close to the side bar lights, (2) that the side and center responses were not sufficiently distinct and could be made simultaneously, and (3) that since biting was the typical coyote behavior perhaps it could be incorporated into the desired response.

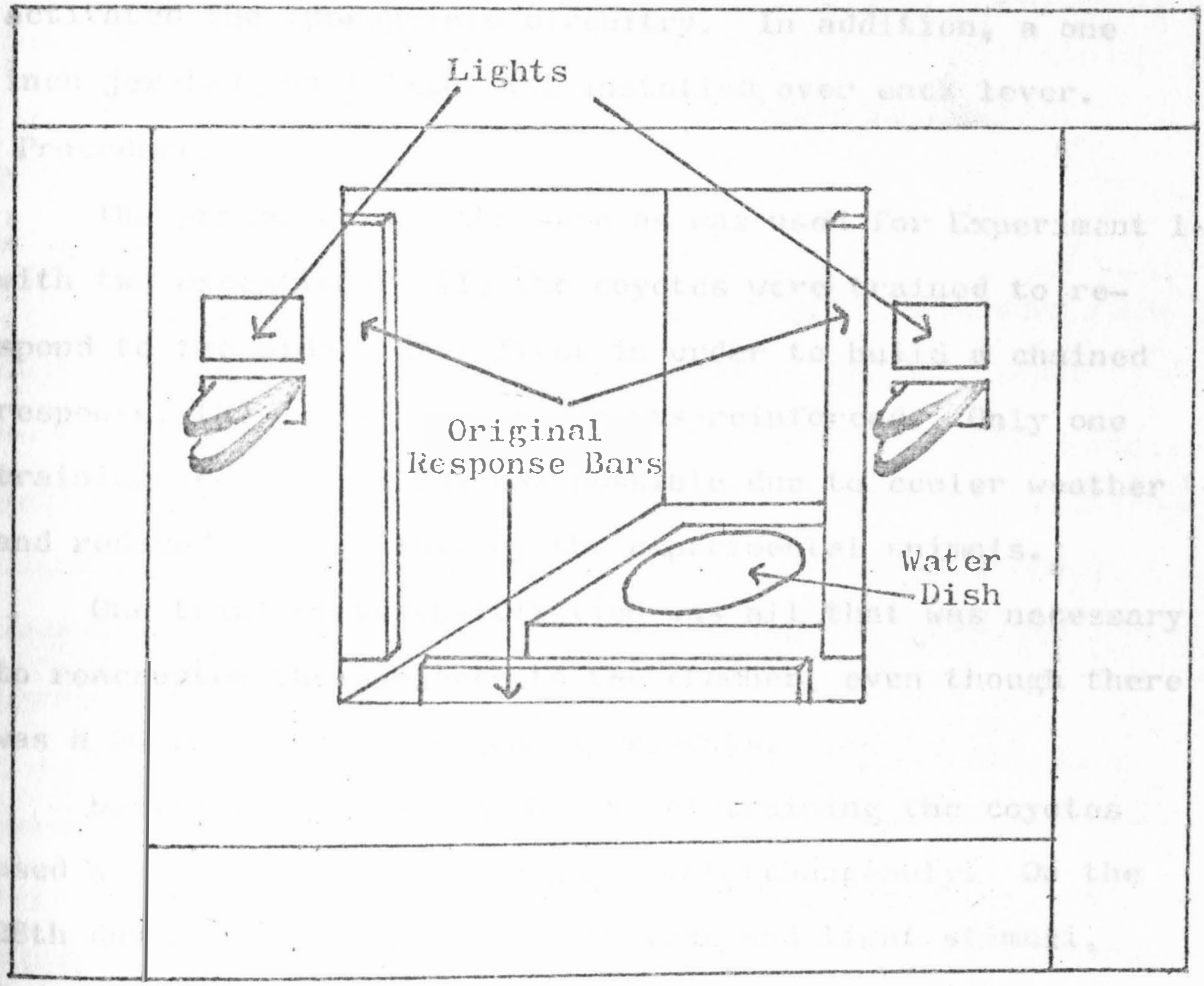
Pilot Experiment 3

Subjects:

Coyotes 1 and 2 were again used in this experiment.

Modified Manipulanda:

In order to make use of the coyote's biting response two additional levers were mounted on either side of the panel opening. (Figure 8) The levers consisted of 6" strap hinges with microswitches mounted on the undersides. The hinges were mounted so that two inches protruded from the face of the response panel. When the subject closed the



Side view of bite levers A and B.

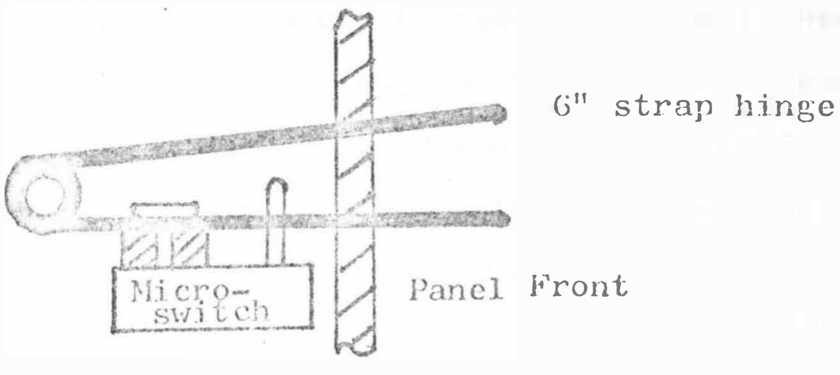


Figure 8. The modified response panel.

hinge flaps with a bite or a paw press, the microswitches activated the appropriate circuitry. In addition, a one inch jeweled panel light was installed over each lever.

Procedure:

The procedure was the same as was used for Experiment 1 with two exceptions: (1) The coyotes were trained to respond to the side lights first in order to build a chained response, (2) A biting response was reinforced. Only one training session per day was possible due to cooler weather and reduced fluid intake by the experimental animals.

One trial of desensitization was all that was necessary to reaccustom the subjects to the chamber, even though there was a 30 day period between experiments.

During the following 30 days of training the coyotes used a bite or paw press response interchangeably. On the 28th day Coyote 1, responding to tone and light stimuli, indicated a "signal trial" with one press to the right lever and a "catch trial" with one press to the left lever. Her typical latency period was 10.36 seconds with a 63% correct response rate. Coyote 2 had achieved a higher level of training, responding to tone stimulus only. Her average latency period was 9.7 seconds with a 63% correct response rate.

Results:

Cold weather forced termination of the training just prior to initiation of test trials.

Concluding Experiment 4

Subject:

The subject was dog 1, the black Labrador used in previous experiments.

Procedure:

Due to the outdoor facilities no experiments were conducted during the winter, so there was a span of eight months between the pilot experiment and the concluding experiment. Because of this time lag the subject was reintroduced to the apparatus and procedure, through a two-week desensitization period in preparation for the training phase.

On May 16, 1976, the training phase began. Sessions were conducted only once each day in the early evening (as opposed to the morning and evening sessions of the pilot experiment.) The hypothesis was that optimmum performance and longer session length were more easily obtained by conducting only one session per day. This was because of the subjects limited daily water intake. The procedure for the first session was as follows: when the bottom bar was illuminated, a response to it illuminated either the left or right bar. A correct response to the illuminated side bar triggered automatic delivery of 20 ml of water reinforcement. "Signal trials" and "catch trials" were presented equally. The dog's correct response rate was 86%, but the session length was only 18 trials. After

10 days the subject had achieved a differential response of 2 presses to the right and 5 to the left. The response was a muzzle press to the right and a paw press to the left. Session length had increased to 30 trials, and correct response rate was greater than 99%.

Starting May 27, a tone stimulus was presented with the illumination of the left bar, while no tone was presented with the illumination of the right bar. After eight sessions with the paired tone and light stimuli the side lights were extinguished and the subject responded only to the illumination of the bottom bar and to the presence or absence of a tone.

For the next two weeks the objectives of the training were to maintain the complete response with a correct response rate of greater than 95% and to increase the number of trials per session. At the end of two weeks the correct response rate was still greater than 95% but the average session length remained at 30 trials. On June 18, in an effort to further increase the number of trials per session, the subject was placed on a partial reinforcement schedule of 80%. This reinforcement schedule increased session length to 43 trials while the correct response rate of 99.5% maintained. As long as the correct response rate remained high it was still possible to reduce the percent reinforcement.

On June 20 the reinforcement schedule was decreased to 70% and to 60% on July 8. At 60% reinforcement the average number of trials was 46 per session. On July 21 the dog was placed on a simulated test schedule of two "catch trials" for every five "signal trials". This simulated test schedule was also designed to obtain an estimate of the subject's thresholds to be utilized in the actual test.

The design of the test schedule was determined by the following factors:

(1) there were 11 frequencies to be tested (.65, 1.25, 2.5, 5, 10, 15, 20, 25, 30, 35 and 40 kHz);

(2) at least 5 replications of each frequency were deemed necessary;

(3) each frequency was to be presented at 5 intensities, varying in 3 dB steps and centered around the estimated threshold;

(4) frequencies were to be presented in high and low blocks due to the use of two acoustic transducers with differing ranges;

(5) an adequate number of "catch trials" were needed as validation trials;

(6) the session length was limited by the number of reinforced trials prior to satiation;

(7) appropriate randomization procedures were required.

The subject's average number of trials per session was 50; therefore, to obtain 5 replications of each frequency and present 5 intensities of each frequency with 13 "catch trials", only 7 frequencies could be presented per session. This yielded 35 "signal trials" and 13 "catch trials" for a total of 48 trials per session. Therefore, seven days were required to complete the test schedule.

The frequencies were separated into high and low blocks and then were randomly selected for order of presentation within each block using six permutations. No more than four frequencies per session were selected from each block. Sessions alternately started with high and low blocks.

In addition three more sessions were added to provide more replications of frequencies judged to be critical. These frequencies were again divided into two blocks; a low block, (.65 and 2.5 kHz), and a high block, (15, 25, 35 and 40 kHz), and randomly presented within each block. The order of the 5 intensities and 1 "catch trial" per frequency was randomly selected from six permutations to eliminate order effects. An additional "catch trial" was placed between each set of frequencies to allow the experimenter time to readjust the frequencies and voltage settings on the apparatus. This 10 day schedule yielded 5 replications of the frequencies .65, 2.5, 15, 25, 35, and 40 kHz, 9 replications of 1.25, 5 and 10 kHz and 10 replications of 20 and 30 kHz, (see appendix C for test schedule.)

Reinforcement for the test sessions was maintained at 70%.

Testing began on July 28 and ended on August 8. Testing was not conducted August 5, because of rain which provided the subject with water and made reinforcement ineffectual.

Results and Discussion:

The dog responded correctly to 99.9% of the "catch trials." Such a high correct response rate to "catch trials" indicated a bias for the no tone response, but also gave reliability to the "signal trials" she did respond to. Therefore, the audiogram derived from this study depicted conservative but reliable estimates of the dog's absolute thresholds.

The audiogram was calculated using graphic and numerical analysis. The data was combined in two different ways. The first was a mean daily audiogram shown in figure 9. The mean daily audiogram was obtained by utilizing a rolling average to estimate the threshold for each frequency each day it was presented. (See appendix E for an example of threshold estimates using a rolling average.)

When the subject responded to all the intensities of a frequency on a given day, the threshold was estimated by subtracting 1.5 dB from the lowest intensity presented. The 1.5 dB value was half of the next 3-dB step. When the

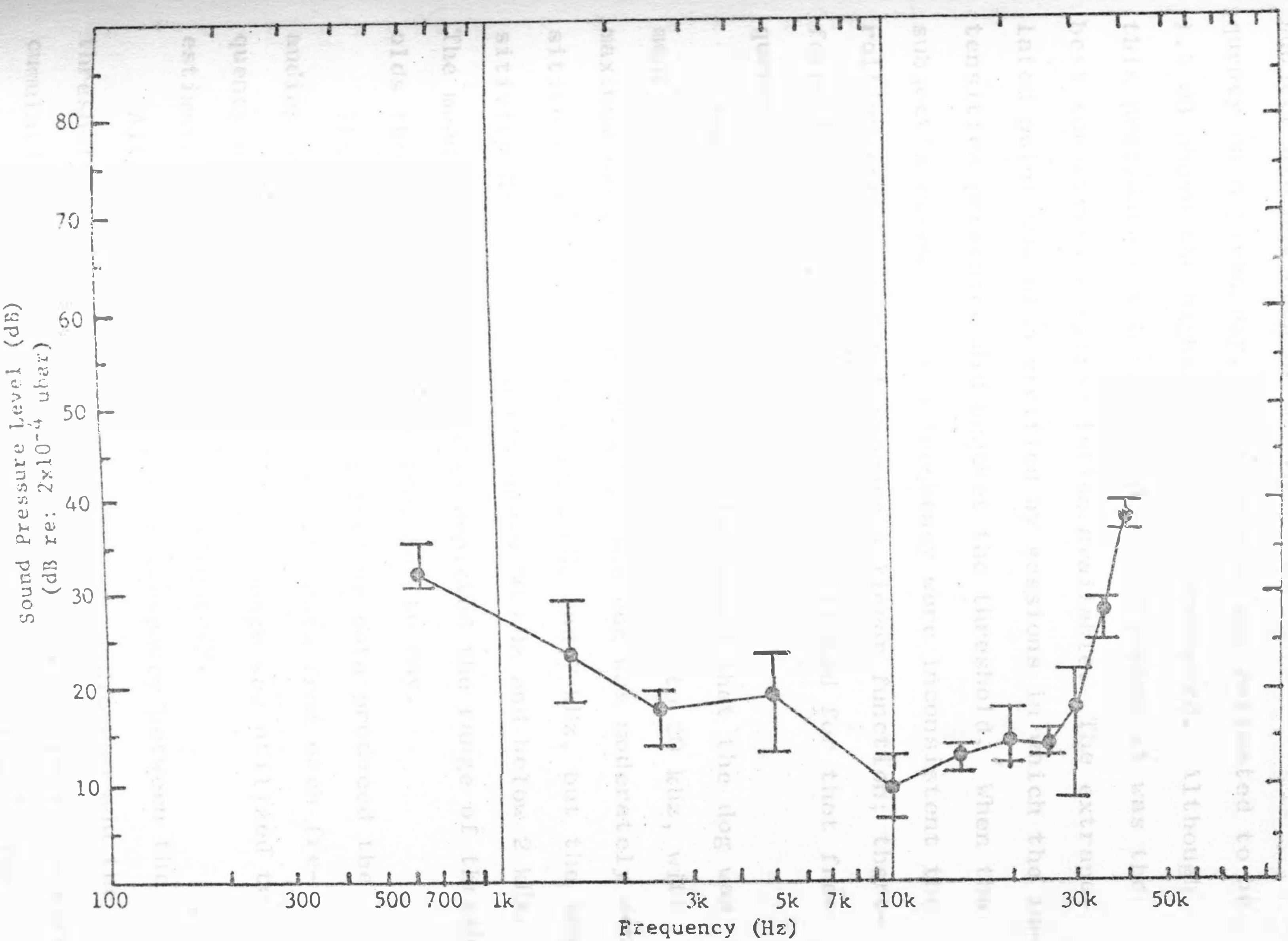


Figure 9. The mean daily audiogram of dog 1.

subject did not respond to any of the intensities of a frequency on a given day, the threshold was estimated to be 1.5 dB above the highest intensity presented. Although this procedure may have biased the estimates it was the best conservative extrapolation available. The extrapolated point was also verified by sessions in which the intensities presented did bracket the threshold. When the subject's responses to a frequency were inconsistent the rolling average did not produce a linear function; therefore, the threshold could not be estimated for that frequency for that particular day.

The mean daily audiogram indicated that the dog was most sensitive to frequencies from 7 kHz to 20 kHz, with maximum sensitivity at 10 kHz. The dog was moderately sensitive to frequencies between 2 kHz and 7 kHz, but the sensitivity diminished rapidly above 30 kHz and below 2 kHz. The mean daily audiogram also depicted the range of thresholds the subject displayed from day to day.

The second way of combining the data produced the audiogram shown in figure 10. The data from each frequency was pooled and a rolling average was utilized to estimate the threshold for the frequency.

Although there was little discrepancy between the thresholds obtained in the mean daily audiogram and the cumulative audiogram there were certain advantages to each. The mean daily audiogram provided threshold ranges for

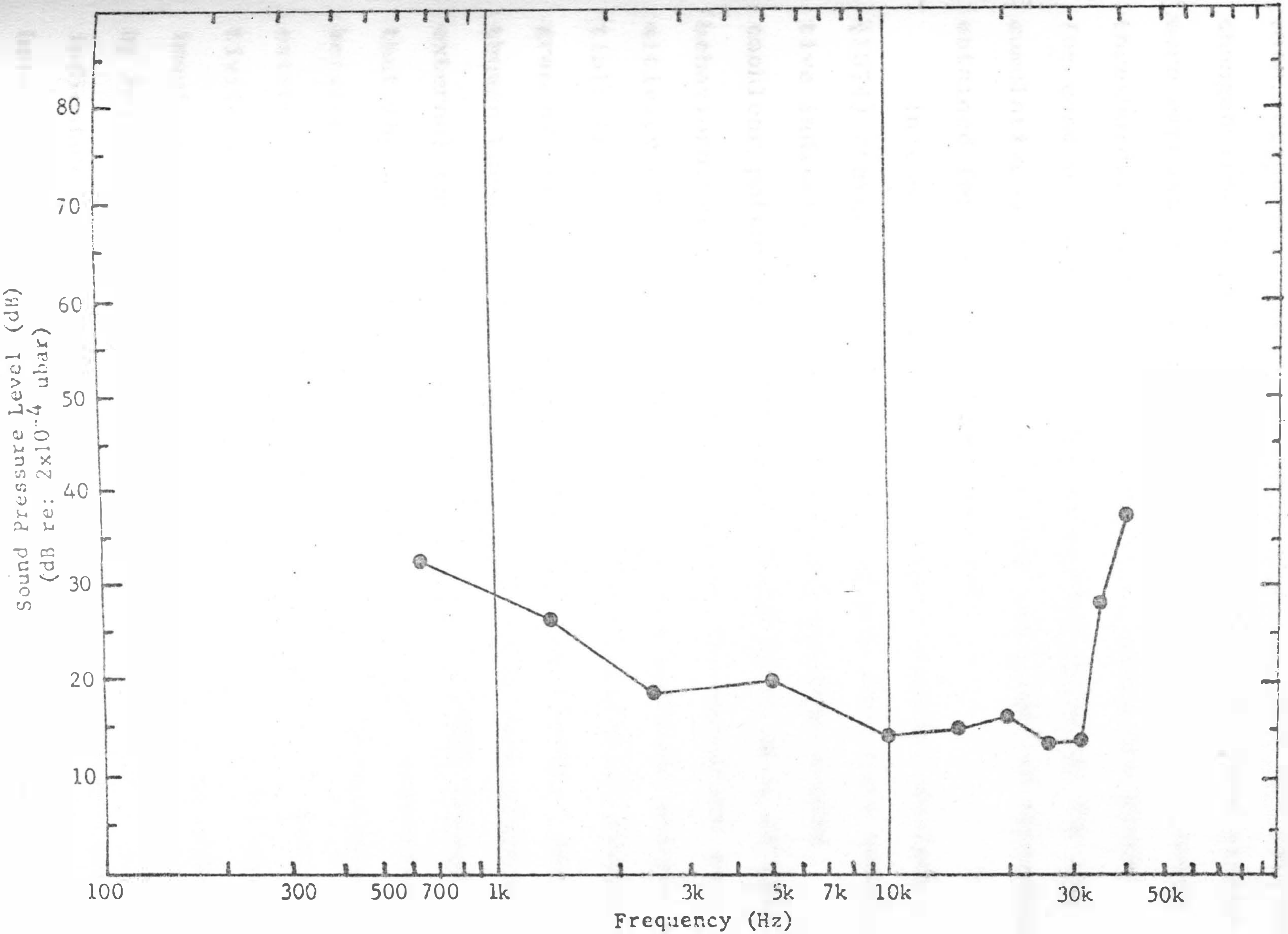


Figure 10. The cumulative audiogram of dog 1.

each frequency. This range indicated how much the threshold changed from day to day. The cumulative audiogram placed more emphasis on the average threshold than on the daily thresholds. In Table 3 the numerical values are given for ease of comparison. The thresholds obtained for the cumulative audiogram are all within the range of thresholds obtained for the mean daily audiogram.

In comparison with other auditory studies, Rasiear (1974) stated that behavioral techniques were more sensitive indicators of auditory sensitivity than evoked cochlear potentials and this was found to be true of this behavioral study. Figure 11 compared the audiotory sensitivity of a beagle obtained by evoked cochlear potentials (Peterson et al., 1966) with the cumulative audiogram of the labrador obtained in this experiment. Although these are two different breeds they have similar external ear structure. Peterson et al. (1966) showed that the auditory sensitivity does not differ appreciably between breeds even when comparing breeds with different external ear structure. Although the pattern of sensitivity was similar the thresholds obtained in this experiment are approximately 40 dB lower than those obtained by Peterson et al. (1966). The behavioral audiogram also indicates more relative sensitivity to the frequencies between 7 kHz and 30 kHz.

Although the behavioral technique used in this study

Table 3

A comparison of the mean daily audiogram and the cumulative audiogram of dog 1.

Frequency (kHz)	Mean Daily Audiogram (dB) (dB re: 2×10^{-4} u bar)	Threshold Range of the Daily Audiogram (dB) (dB re: 2×10^{-4} u bar)	Cumulative Audiogram (dB) (dB re: 2×10^{-4} u bar)
.63	32.0	30-35	32.0
1.25	21.0	18-28	26.0
2.5	17.0	14-19	18.0
5.0	18.0	15-24	19.0
10	9.0	6-13	12.0
15	12.0	11-13	13.0
20	14.0	11-18	15.0
25	13.0	12-15	13.0
30	16.0	8-21	13.0
35	27.0	25-29	27.0
40	37.0	36-40	37.0

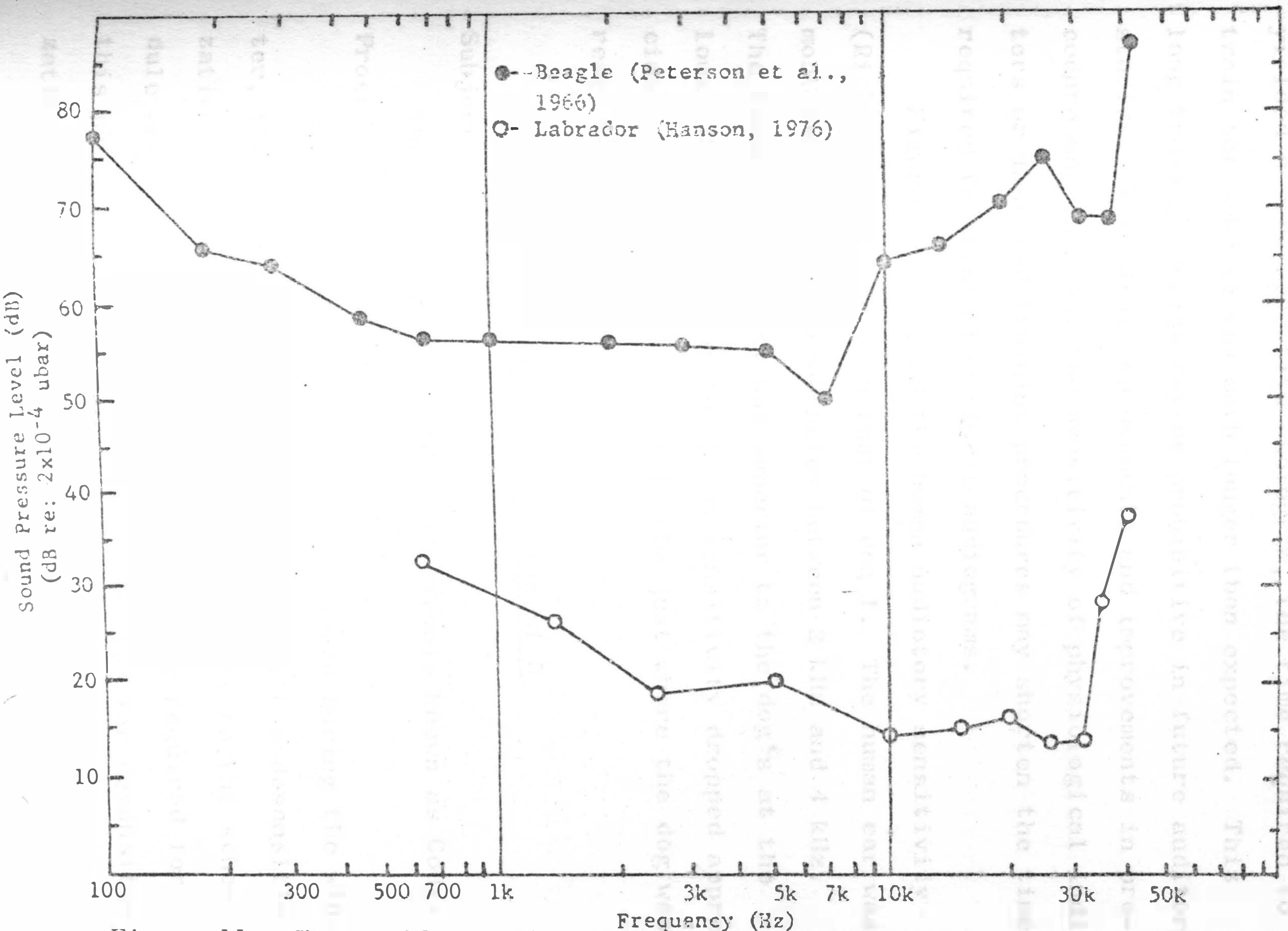


Figure 11. The cochlear potential audiogram of a beagle vs. the behavioral audiogram of a labrador.

yielded a more sensitive audiogram, the time required to train the subject was much longer than expected. This long training period may be prohibitive in future auditory studies. Technical improvements and improvements in procedure may increase the sensitivity of physiological indicators or improved training procedures may shorten the time required to obtain behavioral audiograms.

Figure 12 compared the human audiotory sensitivity (Richardson, 1953) with that of dog 1. The human ear was most sensitive to frequencies between 2 kHz and 4 kHz. The human sensitivity was superior to the dog's at the lower frequencies but the human sensitivity dropped appreciably at frequencies above 10 kHz just where the dog was reaching maximum sensitivity.

Concluding Experiment 5

Subject:

The subject was coyote 1, the female known as Cody.

Procedure:

Since training had been discontinued during the winter, the experiment began May 1, 1976, with a desensitization period. The coyote adapted quickly to the schedule and to the apparatus. The two weeks required for this phase was much shorter than the time for desensitization during the pilot study.

The training phase began on May 13, 1976, utilizing

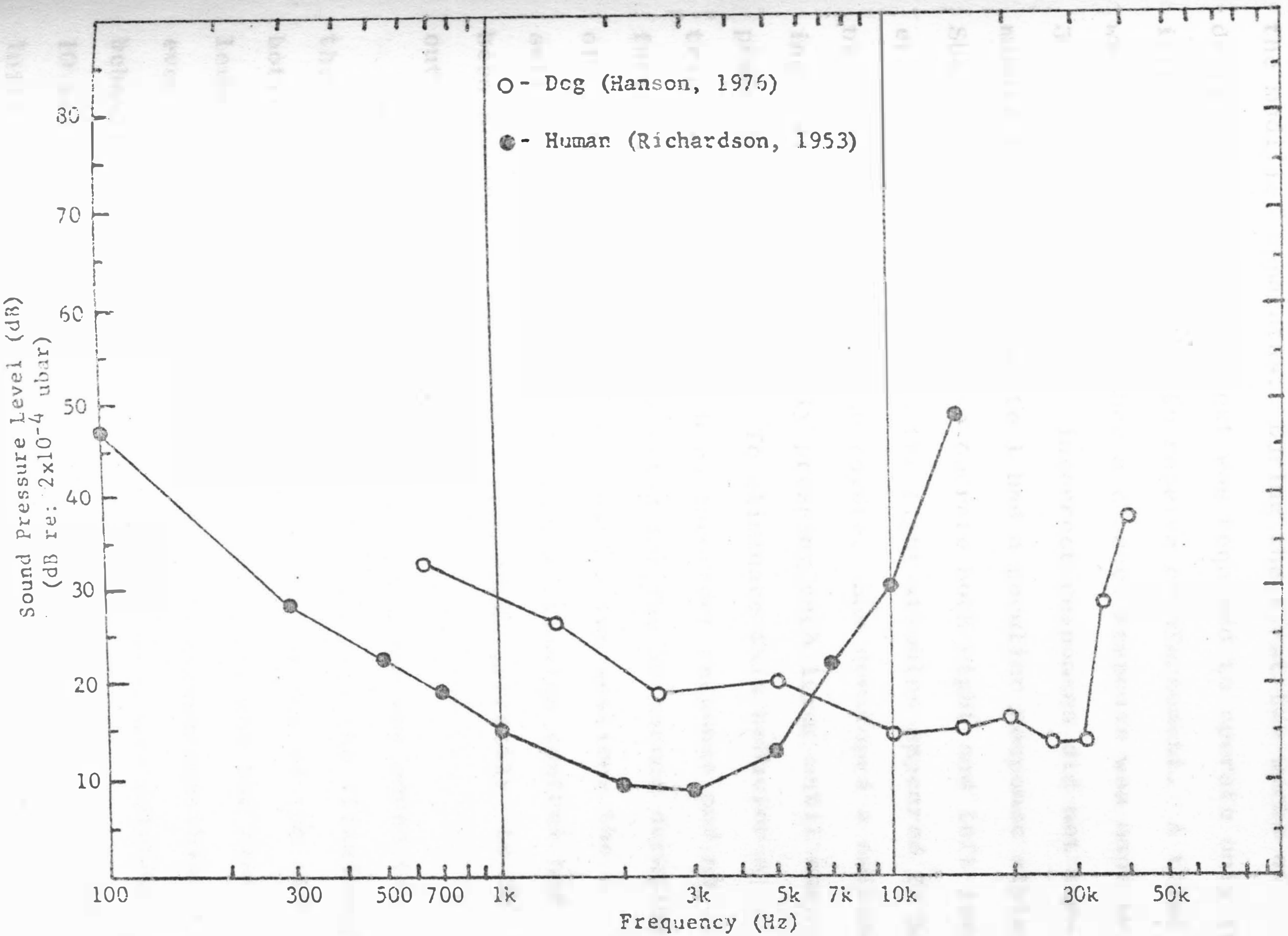


Figure 12. A comparison of auditory sensitivity in man and dog.

the modified apparatus. During the first two weeks of daily sessions the subject was required to operate only the illuminated side lever to receive reinforcement. A trial was terminated when either a correct response was made or 30 seconds had elapsed. Incorrect responses did not terminate the trial. Coyote 1 had a peculiar response style. She used her right paw to operate both right and left levers. With this procedure the light stimulus appeared to have no stimulus value for the coyote. She developed a switching behavior, alternately pressing each lever until one produced reinforcement. To eliminate this behavior a trial was terminated with an incorrect response and no further stimulus was presented for the 30 second duration of the intertrial interval. Within two sessions the switching behavior was stopped and stimulus control had been achieved. The subject responded correctly to 20 out of 22 trials.

On May 31 the illuminated bottom bar was added to the response criteria. Correctly pressing the illuminated bottom bar triggered the illumination of one of the side levers. At first the subject would press the bar readily even when it was not illuminated. To discourage this behavior the 10 second intertrial interval was extended 10 seconds for each incorrect response to the bottom bar. Initially this resulted in some intertrial intervals of over two minutes, but by the 20th of June the behavior was discontinued. The animal pressed the bottom bar only when it was illuminated at the start of a trial.

Starting June 21, the tone stimulus was paired with the illumination of the right lever and no tone was presented with the illumination of the left lever. The required behaviors were two presses on the right lever or one press on the left lever. Session length was 31 trials and there were no incorrect responses. In order to strengthen the behavior this procedure was continued until July 11. At that time the voltage of the side lights was diminished by one half. The side lights were gradually dimmed with each succeeding day until they were completely extinguished on July 28. That session consisted of 50 trials and the animal had a correct response rate of only 74%.

The objective of the training was to achieve a correct response rate consistently above 90%. From July 28 to August 20, the correct response rate varied from 50% to 90%. One problem that kept occurring was the subject's seeming inability to detect the illumination of the bottom bar. The lighting inside the chamber was dimmed to make the bottom bar light more discriminable, but this seemed to have little beneficial effect. In order to make the illumination of the bottom bar more obvious to the subject the control circuit was modified so that the light rapidly blinked on and off. This greatly improved the subject's response to the bottom bar. However, the correct response rate with respect to tone stimulus still averaged 70%.

Some form of punishment for incorrect responses seemed to be the best alternative for improving the correct rate of response. So on July 31, a "time out" period was introduced when the subject made an incorrect response. During the "time out" period no responses were reinforced and all illumination in the chamber was extinguished except for a 25-watt red light. This procedure increased the correct response rate to 80%. However, continued training sessions until September 15, failed to produce a correct response rate higher than 80%.

For the next week the subject was presented a simulated test schedule to accustom her to a reduced number of "catch trials" and to obtain threshold estimates.

The subject's average session length was 65 trials. This allowed 8 frequencies to be tested each day with 5 intensities and 2 "catch trials" presented at each frequency. Frequencies were blocked and randomized as in experiment 4 and one additional "catch trial" was again placed between each set of frequencies. This yielded 40 "signal trials" and 23 "catch trials" for a total of 63 trials per session (see appendix D for test schedule).

Testing began on September 17 and ended on October 7. Testing was interrupted for several days because of rain and furthermore, sessions three through seven were repeated several times because of the subject's substandard performance.

Results and Discussion:

Coyote 1 exhibited a correct response rate to "catch trials" that varied from 14% to 82%. When the correct response rate was high it indicated that the subject was biased toward the no tone response. When the correct response rate was low it was indicative of a bias to the tone response. The average correct response rate was 48.6% so the respective biases seemed to cancel each other, however; this also lowered the reliability of the responses to the "signal trials".

As in experiment 4 a mean daily audiogram and a cumulative audiogram were plotted for coyote 1. The mean daily audiogram (Figure 13) was plotted utilizing a rolling average to estimate the threshold for each frequency each day it was presented. The most sensitive frequency range was 7 kHz to 20 kHz with 10 kHz again the most sensitive. The range of thresholds that the subject displayed from day to day seemed quite large especially at 30 kHz. However, a threshold is not a fixed unchanging point and has been shown to vary with changes in a variety of different conditions including momentary upredictable alterations in the stimulus and the subject itself (Stebbins,

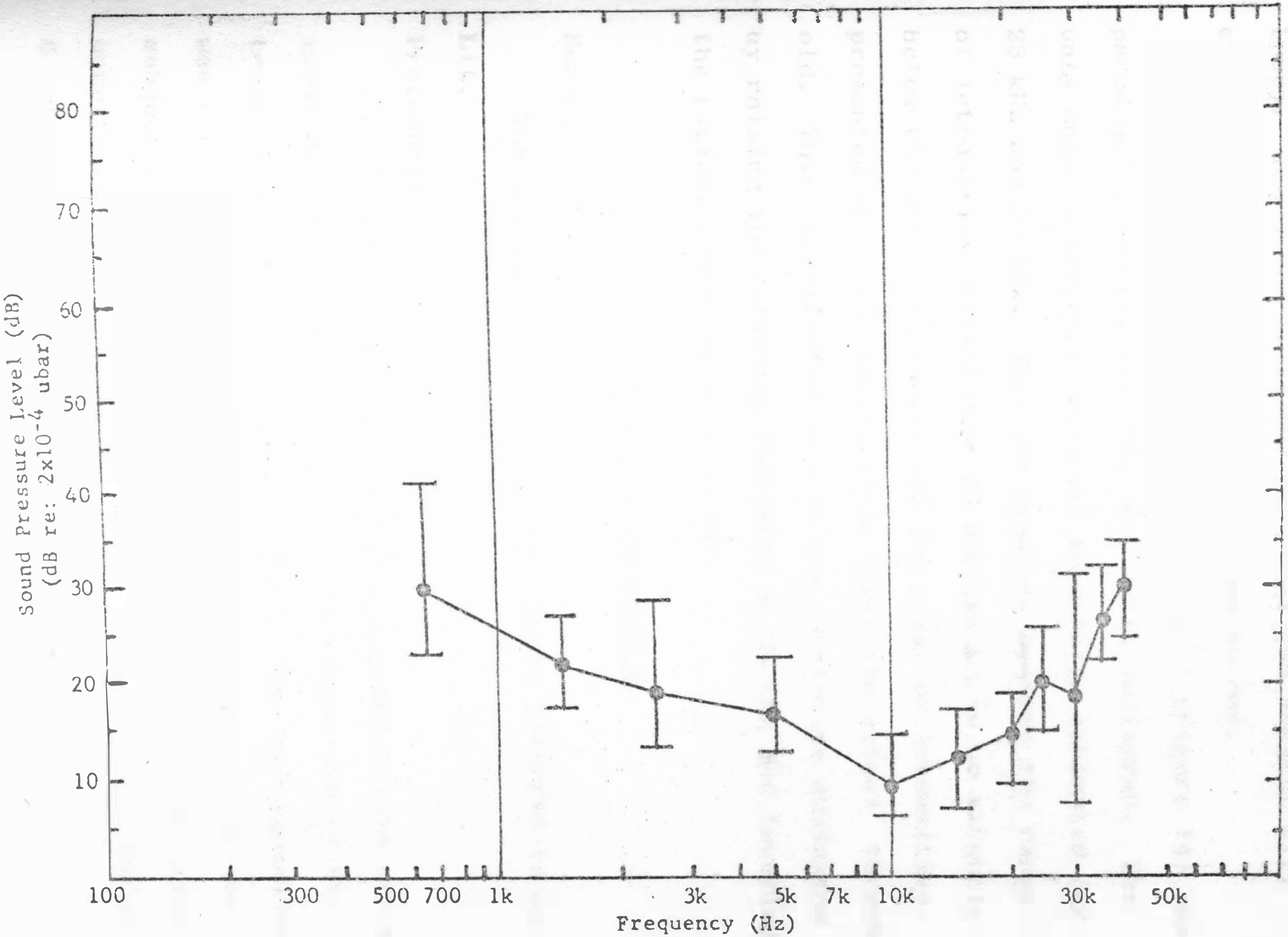


Figure 13. The mean daily audiogram of coyote 1.

1966). Therefore it is expected that the subject will exhibit different thresholds from day to day.

The cumulative audiogram of coyote 1 (Figure 14) compared quite closely with the mean daily audiogram. The only major differences were the thresholds estimated for 25 kHz and 30 kHz. This was probably because the range of intensities presented at 25 kHz tended to be slightly below the actual threshold and the range of intensities presented at 30 kHz tended to be above the actual threshold. This is reflected more in the cumulative audiogram by raising the estimated threshold at 25 kHz and lowering the estimated threshold at 30 kHz.

Concluding Experiment 6

Subject:

The subject was coyote 2, the female referred to as Lil.

Procedure:

Experiment 3 was conducted in conjunction with experiment 2. After the two-week desensitization period the training phase began on May 13, 1976. The same apparatus was used as in experiment 2. For the first session the subject was required to press the illuminated side lever once to receive reinforcement. The subject responded to 6 out of 11 trials but did not drink.

On May 16 the subject was required to press the

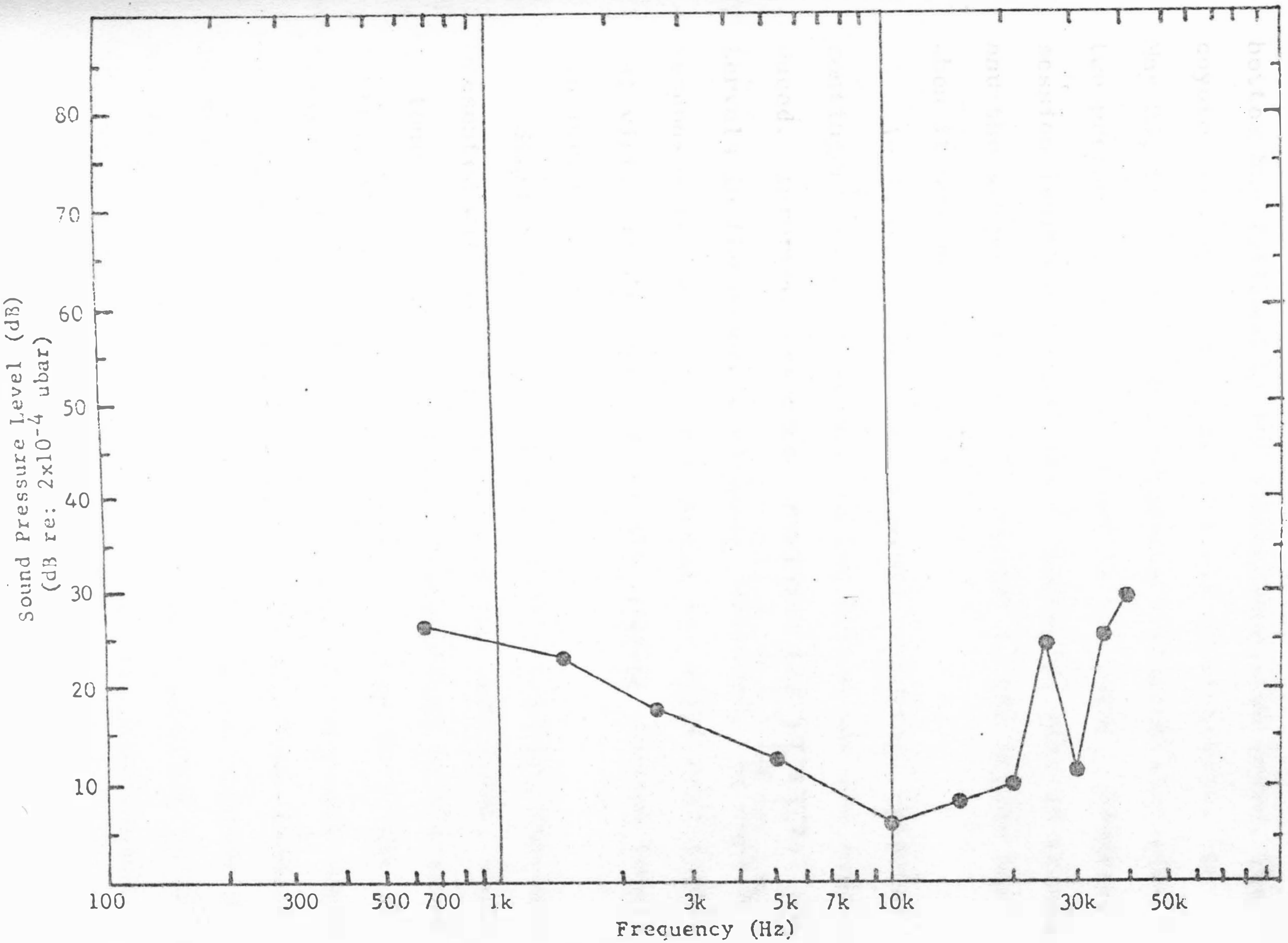


Figure 14. The cumulative audiogram of coyote 1.

bottom bar followed by the illuminated side lever. The coyote responded correctly to 8 out of 15 trials. By May 25, the subject was responding differentially with two presses to the left and one to the right. However, session length was still short, averaging only 15 trials, and the subject continued to respond to the bottom bar when it was not illuminated.

As in experiment 2 a 10-second intertrial interval contingent upon no response to the bottom bar was introduced. Incorrect responses increased the intertrial intervals in the manner previously described. By June 3, responses to the bottom bar during the intertrial interval virtually disappeared and the average session length had increased to 30 trials.

Starting June 5 an easily audible training tone was presented with the illumination of the left lever, while no tone was presented with the illumination of the right lever. The subject correctly responded to 19 of the 26 trials. This procedure was continued for the next month, until July 6 when the voltage of the side lever lights was dimmed by one half. During this session the subject did not respond to 9 trials, but responded correctly to 19 of the remaining 21 trials. By July 10, the side lights had been extinguished and the subject was responding to only the illuminated bottom bar and the presence or absence of tone. The differential response was four bites on the left lever for a "signal trial" and two paw presses to the right for a "catch trial". This session was 75 trials long, but with a correct response rate of only 48%. Continued sessions attempting to improve the correct response rate met with limited success.

On July 31, a "time out" period for incorrect responses was also introduced. This procedure seemed to slightly increase the correct response rate, however, other factors seemed to prevent further improvement.

One factor was that the subject developed a bias in favor of the right response. This was apparently because two paw presses to the right lever were much quicker and easier to execute than four bites to the left lever. To reduce the effect of the bias the number of bites required was reduced to three. The second factor was that the subject had difficulty determining when the bottom bar was illuminated. This resulted in responses to the bottom bar when it was not illuminated. As in experiment 2, a blinking light was used to illuminate the bottom bar. After two weeks the subject's correct response rate averaged 80% and the session length averaged 50 trials.

On September 10 the subject was placed on a simulated test schedule to accustom her to a reduced number of "catch trials" per session and to obtain threshold estimates. A slight bias still existed for the right lever so the number of required responses was reduced to one paw press for the right lever and two bites for the left lever. Session length for the simulated test schedule averaged 62 trials with an average correct response rate of 80%.

Since coyote 2 had an average of 62 trials per session she was tested on the same schedule as coyote 1. Testing of coyote 2 also began on September 17, and ended on October 7. Testing was again delayed by rain and sessions three through seven were repeated because of substandard performance.

Results and Discussion:

Coyote 2 exhibited a correct response rate that varied from 27% to 77%. The average correct response rate to "catch trials" was 45.2% which indicated that the respective biases had cancelled each other, but also indicated that responses to tone trials were not as reliable.

The mean daily audiogram of coyote 2 (Figure 15) was very similar to that of coyote 1. The most sensitive range was again 7 kHz to 20 kHz with the greatest sensitivity at 10 kHz. In general the threshold ranges exhibited by coyote 2 were not as wide as those exhibited by coyote 1. The mean thresholds and the threshold ranges estimated from the mean daily audiogram are given in Table 4 for both coyotes.

In Figure 16 the cumulative audiogram of coyote 2 has been plotted. The major difference between the

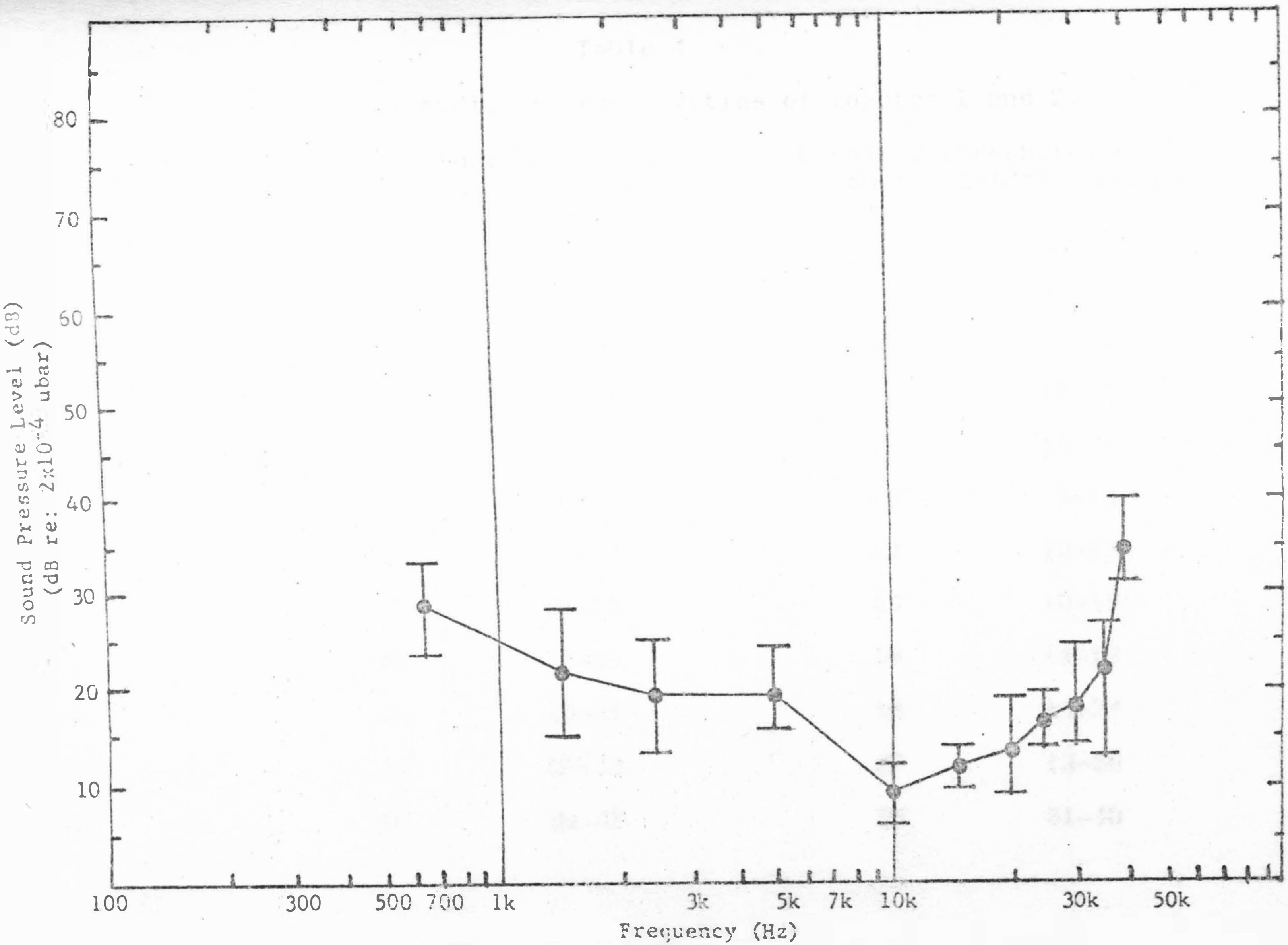


Figure 15. The mean daily audiogram of coyote 2.

Table 4

The mean daily auditory sensitivities of coyotes 1 and 2.

Frequency (kHz)	Coyote 1 Thresholds (dB) (dB re: $2x10^{-4}$ u bar)		Coyote 2 Thresholds (dB) (dB re: $2x10^{-4}$ u bar)	
	Mean	Range	Mean	Range
.63	30	23-40	28	23-33
1.25	22	16-26	21	15-27
2.5	18	13-28	19	13-25
5	17	13-22	19	16-24
10	10	6-15	9	6-12
15	12	7-17	12	10-13
20	15	10-19	13	10-19
25	20	15-26	16	14-19
30	18	13-31	18	14-24
35	26	23-32	23	12-26
40	30	24-35	35	31-40

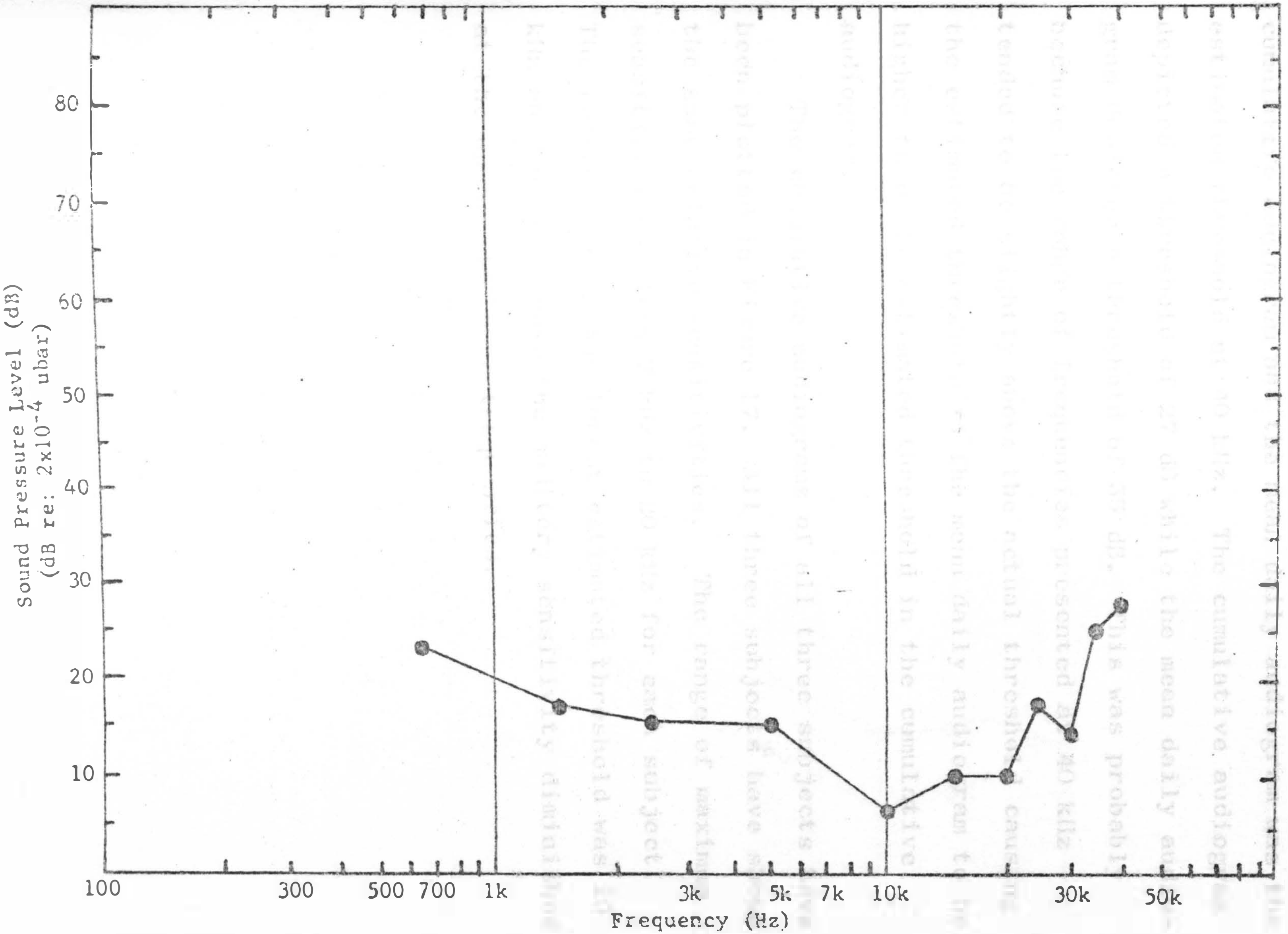


Figure 16. The cumulative audiogram of coyote 2.

cumulative audiogram and the mean daily audiogram was the estimated threshold at 40 kHz. The cumulative audiogram depicted a threshold of 27 dB while the mean daily audiogram depicted a threshold of 35 dB. This was probably because the range of frequencies presented at 40 kHz tended to be slightly above the actual threshold causing the estimated threshold in the mean daily audiogram to be higher than the estimated threshold in the cumulative audiogram.

The cumulative audiograms of all three subjects have been plotted in Figure 17. All three subjects have shown the same relative sensitivities. The range of maximum sensitivity was from 7 kHz to 20 kHz for each subject. The frequency with the lowest estimated threshold was 10 kHz and in every case the auditory sensitivity diminished at the upper and lower frequencies.

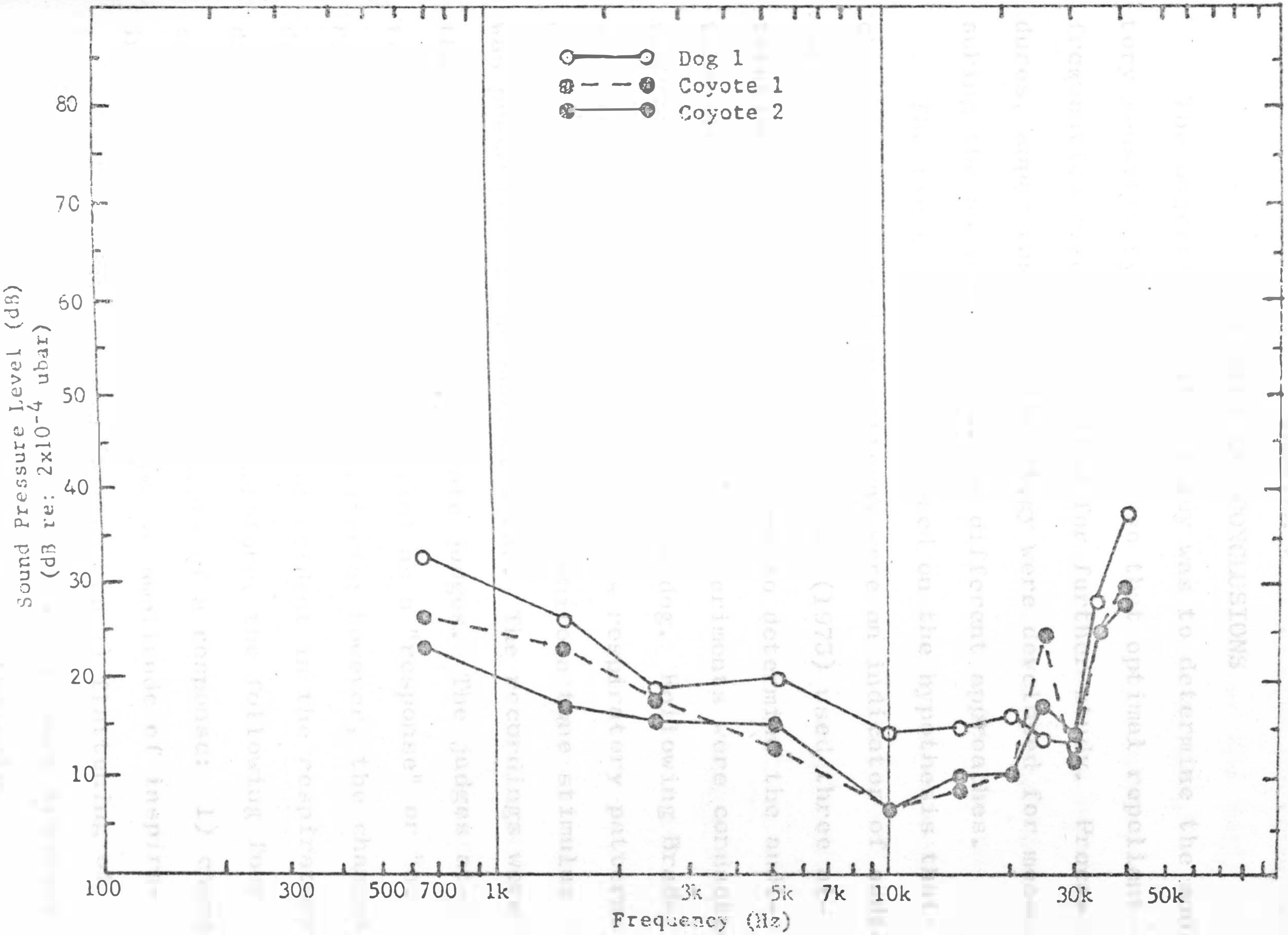


Figure 17. The cumulative audiograms of dog 1, coyote 1, and coyote 2.

CHAPTER V

SUMMARY AND CONCLUSIONS

The objective of this study was to determine the auditory sensitivity of the coyote so that optimal repellant frequencies might be selected for further study. Procedures, apparatus and methodology were developed for measuring the audiogram using two different approaches.

The first approach was based on the hypothesis that changes in respiratory patterns were an indicator of auditory sensitivity. Bradford et al. (1973) used three alterations in respiratory patterns to determine the auditory sensitivity in dogs. Four experiments were conducted two using a coyote and two using a dog. Following Bradford's basic procedure the subject's respiratory patterns were measured via a strain gauge, while a tone stimulus was presented at the subject's ear. The recordings were then examined by three separate judges. The judges attempted to categorize each trial as a "response" or "no response" using Bradford's criteria; however, the changes described by Bradford were not evident in the respiratory data of this experiment. Therefore, the following four criteria were used as indicators of a response: 1) change in respiratory rate, 2) change in amplitude of inspiration, 3) waver during inspiration, or 4) flattening of the inspiration peak. However, even with judge training the judges could not reliably interpret the data.

Therefore, it was tentatively concluded that no inference could be drawn about either the coyote's or the dog's auditory sensitivity from these respiratory data.

The second approach was based on the hypothesis that the audiogram could be determined using operant behavioral techniques. Three subjects were used in this portion of the study, one dog and two coyotes. Although the training took considerably longer than anticipated, using water reinforcement the subjects were successfully conditioned to press one lever when a tone was audible and another lever when it was inaudible.

It was hypothesized that the coyote's maximum auditory sensitivity would approximate that of the dog. The results of the behavioral experiment have shown this to be true. The auditory sensitivity of the dog was very similar to that of the coyote. The dog's thresholds were somewhat higher than those of the coyote, but as stated previously the dog's audiogram was a conservative estimate of her thresholds due to her bias for the no tone response.

The maximum auditory sensitivity of the coyote and the dog was hypothesized to be between .65 kHz and 40 kHz. To test this hypothesis 11 frequencies were presented (.65, 1.25, 2.5, 5, 10, 15, 20, 25, 30, 35 and 40 kHz). The results of the behavioral audiogram indicated that the region of maximum sensitivity was well within this range. Of the frequencies tested, 10 kHz appeared to be by far the most sensitive for both the coyote and the dog. The most sensitive frequency range for the coyote and the dog was from 7 kHz to 20 kHz. Auditory sensitivity was moderate between 2 kHz and 30 kHz but diminished rapidly for frequencies below 2 kHz and above 30 kHz.

In conclusion changes in respiratory patterns were not well defined and could not be reliably categorized by the judges; therefore, no inferences could be drawn about the auditory sensitivity from the respiratory data. Operant behavioral conditioning proved to be a reliable method of determining the coyote's auditory sensitivity, even though the conditioning was lengthened and complicated by the coyote's shy, superstitious behavior. The auditory sensitivity of the coyote closely approximated that of the dog. The range of maximum auditory sensitivity for both the coyote and the dog was between 7 kHz and 20 kHz with the maximum sensitivity at 10 kHz.

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Appendix A

Description of the logic modules

The logic modules were organized according to function and were plugged into a master interconnect board. On the back of this interconnect board, a series of wire-wrap terminals were used to connect between the boards. This method was advantageous when different logic networks were used for different experiments. It was a simple task to remove the wire from one experiment and rewire a new logic sequence on this interconnect board. No soldering or crimping was necessary. This interconnect board also provided power supply voltages to the logic modules plugged into the card edge connectors. Terminals #1, #2, #3, and #4 of each card were reserved for power supply voltages. Therefore, the cards were initially plugged into any connector before final wiring. This allowed flexibility in optimizing module locations for interconnection. The specific cards and their functions have been described below.

Inverter Board: The inverter board contained six logic inverters which were capable of inverting six different logic signals. For example, if the input of inverter #1 was TRUE the output of #1 indicated FALSE, and vice-versa.

AND-Gate Board: This board had four dual input AND gates. The function performed was when both inputs of AND gate #1 were TRUE, the output of gate #1 indicated TRUE. However, when one or both inputs were FALSE, the output indicated FALSE.

4-INPUT AND Gate Board: This board contained two, four-input AND gates. In this case, when the four gate inputs were TRUE, the corresponding output was FALSE. If any one or all inputs were FALSE the output indicated TRUE.

AND-OR Gate: This card contained four, two-input AND gates whose outputs were connected to one four-input OR gate. This card indicated a TRUE on its output if any or all AND gates had their inputs TRUE, and otherwise FALSE.

Counter Board: This board counted the number of input pulses presented to it and provided an output TRUE level when an externally determined number between 1 to 8 pulses occurred. This number was programmed by selective connection of a jumper wire on the board. A reset input was available to restart the count.

Switch Circuit Board: A board with four terminals that switched to +5 volts or 0 volts (ground) was available for interfacing toggle switches with the TTL logic circuits.

Delay: This board provided a TRUE output t seconds (where t could range from 1 to 60 seconds) after the input was TRUE. The value of t was dependent on a predetermined potentiometer value.

Timer and Inverter Board: This board provided a TRUE output for 5 seconds (This time could be varied from 5 to 60 seconds) after an input pulse, and also provided for three inverter functions. The time was determined by a potentiometer setting.

Light Driver Board: This board provided the power to drive 2 individual circuits which supplied power for lights and solenoids from the controller. It accepted a logic TRUE or FALSE and converted that signal to a light ON or it operated a solenoid to provide the water reinforcement. This board provided full-wave or half-wave silicon controlled rectifier (SCR) controlled power for variable power outputs.

Appendix B

Test Schedule for Pilot Study

Trial	Frequency (kHz)	Sound Pressure Level (dB) (dB re: $2x10^{-4}$ u bar)
1	10	25
2	10	30
3	10	35
4	Catch Trial	0
5	10	20
6	Catch Trial	0
7	10	40
8	.65	50
9	.65	35
10	Catch Trial	0
11	.65	45
12	.65	40
13	.65	30
14	5	25
15	Catch Trial	0
16	5	20
17	5	40
18	5	30
19	5	35
20	Catch Trial	0
21	1.25	45
22	Catch Trial	0
23	1.25	40
24	1.25	25
25	1.25	35
26	1.25	30
27	Catch Trial	0
28	15	40
29	Catch Trial	0
30	15	30
31	15	25
32	15	20
33	15	35
34	Catch Trial	0
35	2.5	30
36	2.5	50
37	2.5	35
38	2.5	45
39	2.5	40
40	Catch Trial	0

Appendix C

Test Schedule of Experiment 4

Trial	Frequency (kHz)	Sound Pressure Level (dB) (dB re: $2x10^{-4}$ u bar)
1	1.25	27
2	1.25	15
3	1.25	21
4	1.25	18
5	1.25	24
6	Catch Trial	0
7	Catch Trial	0
8	5.0	23
9	5.0	14
10	5.0	17
11	Catch Trial	0
12	5.0	26
13	5.0	20
14	Catch Trial	0
15	10.0	7
16	10.0	10
17	10.0	19
18	10.0	13
19	Catch Trial	0
20	10.0	16
21	Catch Trial	0
22	1.25	18
23	1.25	27
24	Catch Trial	0
25	1.25	15
26	1.25	24
27	1.25	21
28	Catch Trial	0
29	Catch Trial	0
30	20.0	13
31	20.0	22
32	20.0	16
33	20.0	25
34	20.0	19
35	Catch Trial	0
36	30.0	24
37	30.0	12
38	30.0	18
39	30.0	15
40	30.0	21
41	Catch Trial	0
42	Catch Trial	0
43	20.0	13

Test Schedule of Experiment 4 con't

Trial	Frequency (kHz)	Sound Pressure Level (dB) (dB re: $2x10^{-4}$ u bar)
44	20.0	16
45	20.0	25
46	20.0	19
47	Catch Trial	0
48	20.0	22
49	Catch Trial	0
50	Catch Trial	0

Appendix D

Test Schedule of Experiments 5 and 6

Trial	Frequency (kHz)	Sound Pressure Level (dB) (dB re: $2x10^{-4}$ u bar)
1	.65	35
2	.65	26
3	Catch Trial	0
4	.65	29
5	Catch Trial	0
6	37.9	38
7	31.9	32
8	Catch Trial	0
9	1.25	20
10	1.25	29
11	Catch Trial	0
12	1.25	17
13	1.25	26
14	1.25	23
15	Catch Trial	0
16	Catch Trial	0
17	10	10
18	10	16
19	Catch Trial	0
20	Catch Trial	0
21	10	22
22	10	19
23	10	13
24	Catch Trial	0
25	Catch Trial	0
26	2.5	13
27	2.5	16
28	2.5	25
29	2.5	19
30	Catch Trial	0
31	2.5	22
32	Catch Trial	0
33	Catch Trial	0
34	20	11
35	20	20
36	Catch Trial	0
37	20	14
38	20	23
39	20	17
40	Catch Trial	0
41	30	28
42	30	16
43	30	22
44	Catch Trial	0

Test Schedule of Experiments 5 and 6 con't

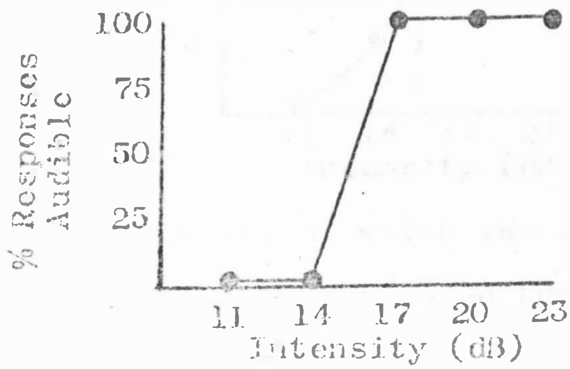
Trial	Frequency (kHz)	Sound Pressure Level (dB) (dB re: $2x10^{-4}$ u bar)
45	30	19
46	30	25
47	Catch Trial	0
48	Catch Trial	0
49	35	27
50	35	36
51	Catch Trial	0
52	35	24
53	35	33
54	Catch Trial	0
55	35	30
56	Catch Trial	0
57	40	34
58	40	25
59	40	28
60	Catch Trial	0
61	40	37
62	40	31

Appendix E

Auditory thresholds estimated using a rolling average

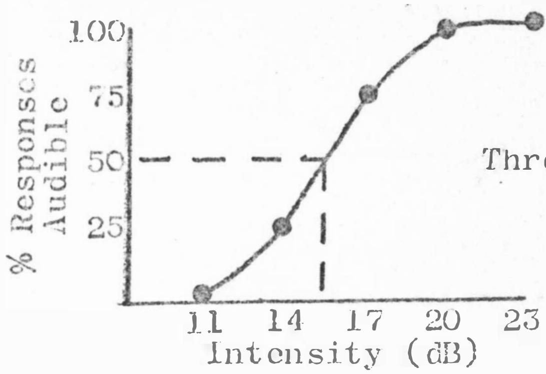
To estimate the threshold for a frequency on a given day, the subject's responses were first plotted graphically. A response indicating an audible tone equalled 100% and a response indicating an inaudible tone equalled 0%.

Frequency (kHz)	Intensity (dB) (dB re:2×10^{-4} u bar)	Response
20	20	audible
20	11	inaudible
20	23	audible
20	14	inaudible
25	17	audible



Each data point was multiplied by 2 and the two data points on either side were added to the product. This sum was then divided by four and the quotient was plotted as the rolling average value for that intensity. Data points on the ends were multiplied by 2, the product was added to the value of the data point next to it and this sum was divided by three.

Intensity (dB) (dB re: 2×10^{-4} u bar)	Rolling Average
11	$\frac{2(0) + 0}{3} = 0\%$
14	$\frac{2(0) + 0 + 100}{4} = 25\%$
17	$\frac{2(100) + 0 + 100}{4} = 75\%$
20	$\frac{2(100) + 100 + 100}{4} = 100\%$
23	$\frac{2(100) + 100}{3} = 100\%$



Threshold = 15.5 dB

The intensity at which the frequency was audible 50% of the time was the estimated threshold.